

REVISION OF NORTH AMERICAN SPECIES OF
ILYBIUS ERICHSON (COLEOPTERA: DYTISCIDAE),
WITH SYSTEMATIC NOTES
ON PALAEARCTIC SPECIES

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Abstract.—Adults of the North American species of the holarctic genus, *Ilybius* Erichson, are reviewed, and keys for their recognition, descriptions, and maps of distributions are presented. Fourteen species are recognized. The following new synonymies are proposed: *Ilybius laramaeus* LeConte is a junior synonym of *I. biguttulus* Germar; *I. denikei* Wallis is a junior synonym of *I. confusus* Aubé; and *I. suffusus* Crotch is a junior synonym of *I. subaeneus* Erichson. The genus is primarily northern, with the majority of species in the northern Appalachian and boreal regions. Four species are holarctic.

The distribution of character states among species is discussed and a cladogram is presented for North American species. Two subgenera are recognized: *Agabidius* Seidlitz with two species in Asia; and *Ilybius* s. str. to which all North American species are assigned. Although not included in the cladogram, the distribution of character states among Palearctic species is discussed and the positions of these species in the cladogram are noted.

SYSTEMATIC POSITION OF *ILYBIUS* ERICHSON

The genus *Ilybius* is one of the more sharply defined genera within the dytiscid subfamily Colymbetinae. Characteristics of the genus are given by Leech (1942) and Leech and Chandler (1956) in the key to North American genera of Dytiscidae, and a description of the genus is given by Larson (1975).

Although *Ilybius* is well defined, its systematic position has been debated. Most authors follow Sharp (1882) in assigning *Ilybius* to the tribe Agabini. Zimmermann (1935) (followed by Zaitzev, 1953) placed *Ilybius* in the tribe Colymbetini due to the unequal metatarsal claws and the apically lobed metatarsomeres in contrast with the equal metatarsal claws and non-lobed metatarsomeres of members of his tribe Agabini. However, he did point out that species of *Ilybius*, like members of the tribe Agabini but unlike other members of Colymbetini, possessed a linear arrangement of short setae on the posteroapical angle of the metafemur. Balfour-Browne (1950) reviewed the characters of *Ilybius* and showed that a phenocline in the lobing of the hind tarsi could be found among members of the genera *Agabus* Leach and *Ilybius*, an observation made in a more general way by Sharp (1882). In addition, some *Agabus* species show an inequality in the relative lengths of the two metatarsal claws while some *Ilybius* species have metatarsal claws that are almost equal. *Carrhydrus crassipes* Fall, which has very unequal metatarsal claws, has many affinities with members of *Agabus* s. str. (Leech, 1942; Larson, 1975) and probably represents a sister group of this subgenus. Metatarsal claw length is unstable even between closely related forms. Sharp (1882:891) noted that in characters of the hind legs of *Ilybius* species "there are scarcely two species which agree exactly in the size and form of their parts" (lobing of metatarsomeres, leg width, hind coxa and metasternal wings).

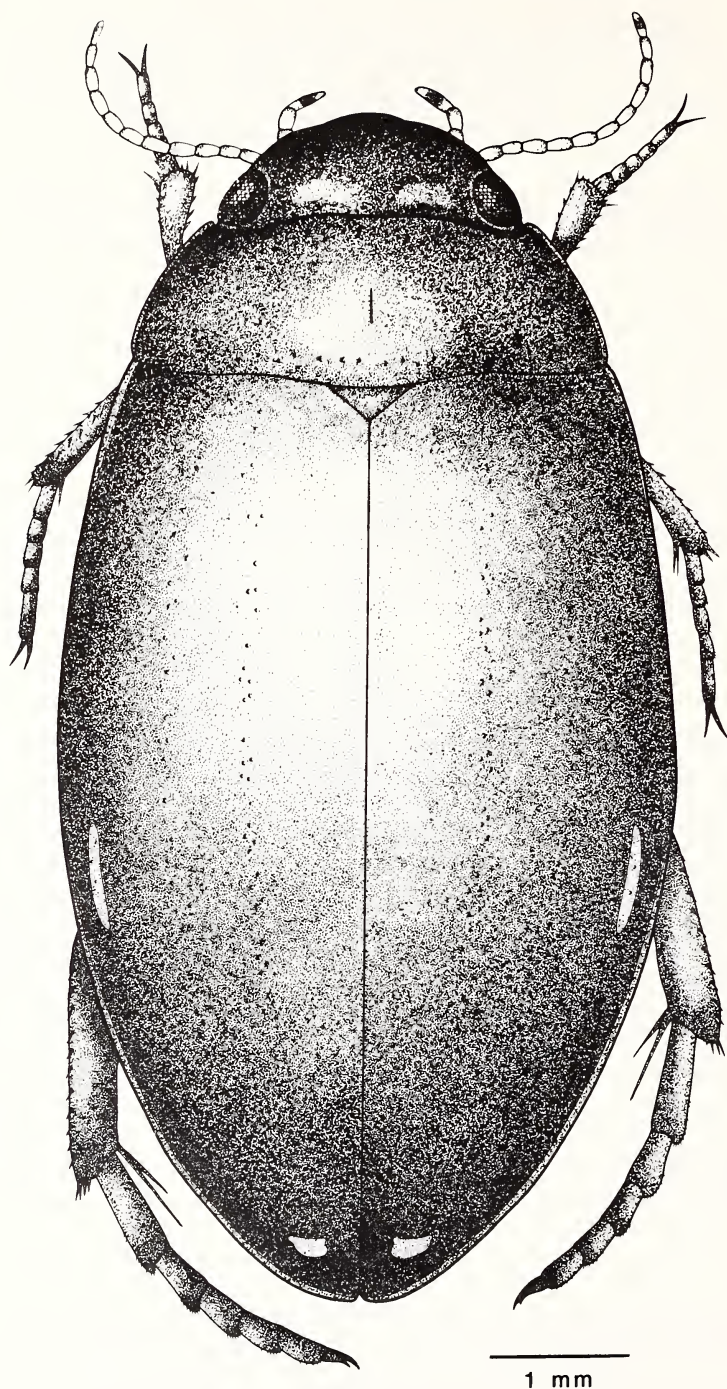


Fig. 1. Habitus of *Ilybius angustior* (Gyllenhal).

In fact, the great similarity between certain members of *Agabus* and *Ilybius* is exemplified by the holarctic *I. vittiger* (Gyllenhal), being treated as a species of *Agabus* until recently when it was independently recognized as a species of *Ilybius* by Larson and Roughley (1983) and Nilsson (1983).

There is strong similarity between adults of *Ilybius* and *Agabus* in the structure of the proventriculus (Balfour-Browne, 1934), pleurites of abdominal segment 2 (Leech, 1942), and wing venation (Goodliffe, 1939). Dettner (1985) placed *Ilybius* in the Colymbetini, but the pygidial gland constituents he listed for *Ilybius* species show as much similarity to those of various *Agabus* and *Platambus* Thomson species as they do to any member of the Colymbetini. However, Dettner found *Ilybius* to be characterized by the possession of tiglic acid as one the pygidial gland components, further emphasising the isolated position of the genus.

Brinck (1948) reviewed morphological characters used in the classification of the genera of Colymbetinae and demonstrated that no single character has been discovered that will define adults of the tribe Agabini or Colymbetini. Nevertheless, he concluded that the weight of evidence indicated a closer relationship of *Ilybius* with *Agabus* than with any members of the tribe Colymbetini.

A close relationship between *Agabus* and *Ilybius* is also indicated by the larvae. Nilsson (1983) concluded "no character has been found for the separation of the larvae of these genera that is valid for all species and all three instars." Nilsson (1983) introduced the relative width of the sclerotized parts of the ventral surface of abdominal sternum 6 and relative positions of setae and stigmata as characters to separate 3rd instar larvae of *Agabus* and *Ilybius*. These characters are gradational, as are the ridging of the side of the head and the setae of the fore femur used by other authors (Balfour-Browne, 1950; Leech and Chandler, 1956; Galewski, 1966), and do not show sharp discontinuities between the groups.

I concur with Sharp (1882), Leech (1942), Brinck (1948) and Balfour-Browne (1950) in placing *Ilybius* in the tribe Agabini because of the general similarity in adult and larval structure between members of *Ilybius* and certain species of *Agabus*, and the shared possession of the metatibial comb which is not found in a similar form among members of the tribe Colymbetini.

Within *Agabus*, it is the species of the *A. chalconatus* group of Zimmermann (1935) that appear most similar to members of *Ilybius*. Among these species, the metatarsi are relatively broad, the posteriolateral angles of the metatarsomeres are more or less lobed and the metatarsal claws are slightly unequal and dissimilar in shape. In some species, notably *A. neglectus* Erichson, the basal two or three metatarsomeres are longitudinally impressed dorsolaterally so that a more or less evident convexity or ridge exists along the dorsolateral margin of the tarsomere, reminiscent of the externolateral beading of the metatarsomeres of males of many *Ilybius* species. *Agabus chalconatus* (Panzer) has sucker hairs on the inner face of the parameres as do many species of *Ilybius*. The character state is also found in a few other species of *Agabus* not belonging to the *A. chalconatus* group (Balfour-Browne, 1950). Other points of similarity exist between individual members of the *A. chalconatus* group and certain species of *Ilybius*, but no synapomorphy is known to indicate they are sister groups. The female gonocoxae, while elongate, sclerotized and with reduced setae in members of the *A. chalconatus* group, are not dorsally toothed and female sternum 6 is not medially emarginate as in all species of *Ilybius*. The ovipositor is uniform among members of *Ilybius* and consistently different from that of any other Colymbetinae.

With few exceptions, members of *Ilybius* share a characteristic habitus (Fig. 1) which, even in the field, provides a reliable guide for recognition. The species are of moderate size. The body is oval in dorsal aspect, generally widest behind the middle, and relatively strongly narrowed towards both the anterior and posterior ends: in the lateral aspect the beetles are strongly convex dorsally and flattened ventrally. The color is usually dark although many specimens have the lateral margins of the body and the appendages variously paler. A medial sublateral pale vitta and a subapical pale spot are generally present on each elytron. The pale markings may not be visible on all specimens either because the pale areas are very faint and only discernable when the elytron is lifted and examined against a light, or because the lateral pale areas are expanded mesad to incorporate the pale spots. Also, such maculations are characteristic of a number of other agabines.

The single best generic character is the structure of the female genitalia. A saw-like ovipositor is formed by the gonocoxae which are laterally flattened, sclerotized and narrowly triangular in shape with the dorsal surface of the pointed apex bearing a row of prominent teeth (Jackson, 1960; Burmeister, 1976). Associated with this form of ovipositor is an emargination of the posteriomedial portion of sternum 6, presumably to permit extrusion of the gonocoxae and permit their vertical movement. The form of the ovipositor so perfectly resembles a key-hole saw that an immediate conclusion is that it functions to cut slits into substrates in which eggs are deposited. In fact, this has been observed by Jackson (1960) who described the structure of the ovipositor and mechanism of oviposition which involves depositing eggs into slits cut into the stems of aquatic plants.

The homogeneity of the genus shows in its nomenclatural history. Since Erichson (1832), there have been few generic synonyms proposed and little confusion in species placement. Although I have not examined the type species, the Palaearctic genus *Colymbinectes* Falkenstrom, 1936, appears very similar to species of *Ilybius* and was considered to be a synonym of *Ilybius* by Gschwendtner (1939). Zaitzev (1953) recognized *Colymbinectes* but admitted specimens differed from those of *Ilybius* only in their broader hind tarsi. However, Brinck (1948) reported that the gonocoxae of *Colymbinectes* differ from those of *Ilybius* so that *Colymbinectes* is not a synonym of *Ilybius*. The remaining genus group names listed in the following synonymy were all proposed for subgenera.

Although the high level of similarity among species has facilitated generic assignment of species, it has caused considerable difficulty in species recognition. Fall (1927) and Wallis (1939) presented keys to the North American species with which it is possible to identify most males, but many females cannot be identified to species because intraspecific variation is greater than appreciated by those authors. The lack of extensive descriptions, illustrations and reference to genitalic characters makes these works difficult to use. The key to species presented by Larson (1975) included new characters and was augmented by descriptions, but covered only part of the North American fauna.

ECOLOGY OF *ILYBIUS*

Larson (1975) and Larson and Colbo (1983) described the habitats of adults of northern and western species, but nothing has been published on the habitats of several eastern North American species. Adults are primarily lentic in habitats which

range from tiny bog pools to the protected shorelines of large lakes (Larson, 1985; Ranta, 1985). Although some species occur in habitats that dry for short periods of time, no North American species is typically an inhabitant of short-lived water bodies such as vernal ponds. Larson (1985) observed that the species of northwestern North America tend to be segregated along gradients seemingly correlated with temperature and seasonal history of water bodies and with major terrestrial vegetation types.

Considerably more is known about the life history of European species, due especially to the work of Balfour-Browne (1950), Jackson (1960), Galewski (1966) and Nilsson (1981, 1983, 1986). The life histories of all European species follow a pattern unique among agabines. Nilsson (1986) describes the life history as semivoltine, proceeding as follows: eggs laid in summer hatch quickly into overwintering larvae which pupate the next spring or summer and develop into adults which overwinter before ovipositing in their third summer. Both adults and larvae can be found together over much of the year. Larvae overwinter in ponds while at least some adults apparently overwinter on land (Wesenberg-Lund, 1912; Jackson, 1960). Life history patterns may vary geographically. Dr. Wm. Hilsenhoff (1986, in litt.) has found, over many years of water beetle collecting in Wisconsin, few adult specimens of *Ilybius* in the spring until June which was the month in which he collected most specimens. Also, the vast majority of teneral adults were collected in June. Adult collections then gradually declined over the summer. Hilsenhoff interprets this pattern as indicating a univoltine life cycle with adults emerging in late spring, then mating and ovipositing in summer. The majority of adults then apparently die although some adult overwintering occurs. Larvae hatch in summer and fall and overwinter.

Larvae of all holarctic species have been described (Galewski, 1966; Nilsson, 1981, 1982, 1983). Larvae of the endemic nearctic species are unknown.

METHODS AND MATERIALS

The methods and taxonomic terms used are those of Larson (1975). Species are recognized on the basis of discontinuities in the distribution of character states. The members of several species pairs differ subtly in only two or three characters. However, as these differences were observed to be consistent within areas of sympatry, it was interpreted that maintenance of difference was due to genetic isolation of species. Geographical variation in certain characters was observed in several species, but in no instances were geographical populations of a species sharply enough delimited morphologically to be given formal infraspecific ranking.

Measurements important for species recognition are:

- total length (L)—measured from apex of clypeus to apex of elytra;
- width (W)—maximum width of body across elytra: the ratio L/W is used as an index of shape;
- width of metasternum (WS)—the side piece of the metasternum is wing-shaped and is referred to as the metasternal wing. The measurement is taken across the metasternum at point of closest approximation of mesocoxal cavity to metacoxa. This measurement does not include width of the narrow bead around the mesocoxal cavity, in this respect differing from measurements given earlier (Larson, 1975; Larson and Roughley, 1983). Change in measurement was adopted because leg position and dirt on the specimen less frequently obscure the reference

point for measurement when the mesocoxal bead is excluded. The coxal bead is rather uniform among species and does not offer useful characters;

- width of metacoxa (WC)—measured along an extension of line along which measurement WS was taken. The relative widths of WS and WC are expressed as the ratio WC/WS. Values for ratios are a little larger than those previously published because of the change in the measurement of WS.

Literature references are restricted to citations of original descriptions of North American and select Palaearctic taxa, comprehensive studies on the genus, and recent papers. Much of the early Palaearctic literature and synonymy is cited by Zimmermann (1920) and Balfour-Browne (1950).

The genus is well represented in North American collections. The majority of specimens examined came from the Canadian National Collection, Ottawa (CNC), California Academy of Sciences, San Francisco (CAS), and the United States National Museum, Washington (USNM). Additional specimens were examined from:

Academy of Natural Sciences of Philadelphia (ANSP);
British Museum (Natural History), London (BMNH);
B. & J. Carr Collection, Calgary (CARR);
C. Chantal Collection, Sept-Iles (CHANT);
Memorial University of Newfoundland, St. John's (MUN);
Museum of Comparative Zoology, Harvard University (MCZ);
New Mexico State University, Las Cruces (NMSU);
Nova Scotia Provincial Museum, Halifax (NSPM);
Old Dominion University, Norfolk, Virginia (ODU);
Peabody Museum, Yale University (PMYU);
Royal Ontario Museum, Toronto (ROM);
Cook College, Rutgers University, New Brunswick, New Jersey (RU);
University of Alberta, Strickland Museum, Edmonton (UASM);
University of British Columbia, Vancouver (UBC);
University of Montreal Collection, Montreal (UMC);
Zoologische Staatssammlung, Munich (ZSM).

An attempt was made to examine all North American types. However, the following types could not be located: *I. biguttulus* Germar (repository not located); *I. confusus* Aubé and *I. quadrimaculatus* Aubé (specimens searched for in Institut Royal des Sciences Naturelles de Belgique but not located); and *I. viridianeus* Crotch (not located in either ANSP or MCZ collections).

Collection records for all species are indicated on distribution maps, but, in order to save space, detailed collection data are not presented. These data are available from the author on request. An emphasis was placed on examination of specimens from Canada and the northeastern portion of the continent as these are the regions in which the major taxonomic problems were noted. The treatment of the genus in the western United States is somewhat cursory as there appear to be only a few well defined species in the region.

The BMNH, CAS, CNC, MUN and UASM also contain specimens of palaearctic *Ilybius*, of which I examined specimens of: *I. aenescens* Thomson, 1870; *I. angustior* (Gyllenhal, 1808); *I. apicalis* Sharp, 1873; *I. ater* (DeGeer, 1774); *I. cinctus* Sharp,

1882; *I. crassus* Thomson, 1856; *I. fenestratus* (Fabricius, 1781); *I. fuliginosus* (Fabricius, 1792); *I. guttiger* (Gyllenhal, 1808); *I. lateralis* (Gebler, 1832); *I. meridionalis* Aubé 1838; *I. obtusus* Sharp, 1882; *I. quadriguttatus* (Lacordaire, 1835); *I. similis* Thomson, 1856; *I. subaeneus* Erichson, 1837; *I. vittiger* (Gyllenhal, 1827) and *I. weymarni* Balfour-Browne, 1947.

Ilybius Erichson, 1832

Ilybius Erichson, 1832:18, 34. Type species *Dytiscus fenestratus* Fabricius, 1781:294, designated by Westwood, 1838:8.

Ilyobius Gemminger and von Harold 1868:451 (unjustified emendation of *Ilybius* Erichson).

Idiolybius des Gozis, 1886:8. Type species *Dytiscus fenestratus* Fabricius, 1781:294.

Agabidius Seidlitz, 1887:97. Type species *I. cinctus* Sharp 1882:560, designated by Guignot 1948:169.

Ilybidius Guignot, 1948:167. Type species *I. discedens* Sharp, 1882:557, by monotypy.

KEY TO ADULTS OF NEARCTIC SPECIES OF *ILYBIUS*

- I. Pro- and mesotarsomeres 1–3 slightly broadened and bearing long-stalked, oval, yellow suckers beneath: sternum 6 with hind margin broadly rounded, truncate or slightly concave but not narrowly emarginate medially Key A, males
- II. Pro- and mesotarsomeres lacking ventral suckers: sternum 6 with a narrow medial emargination or notch on hind margin Key B, females

KEY A. MALES

- 1. Metatarsomeres 1 to 4 each with a ridge along dorsoexternal margin 2
- Metatarsomeres lacking ridge or bead 7
- 2(1). Sternum 6 with a number of coarse longitudinal rugae or striae on posterior surface, setiferous punctures more or less obscured by rugae; a narrow, longitudinal posteriomedial keel present or not 3
- Sternum 6 more or less smooth or faintly rugose along posterior margin, setiferous punctures evident; a longitudinal posteriomedial keel present ... *pleuriticus* LeConte
- 3(2). Sternum 6 with a posteriomedial keel: antenna with at least apical flagellomere infuscate medially 4
- Sternum 6 lacking posteriomedial keel but posterior surface with strong longitudinal rugae; antenna entirely yellow, without apical infuscation ... *subaeneus* Erichson
- 4(3). Metatibia with coarse punctation restricted to basal 1/3 to 1/2, remainder of ventral face finely punctate: aedeagus with apex spear-shaped in dorsal aspect (Fig. 70) *quadrimaculatus* Aubé
- Metatibia with coarse punctation along length of ventral face: aedeagus evenly narrowed to apex 5
- 5(4). Size small, L—7.1 to 8.6 mm (population means < 8.0); metasternal wing narrow, WC/WS—2.4 to 3.6 (\bar{x} > 2.6); body narrow, L/W—1.89 to 2.07 (\bar{x} > 1.94): aedeagus slender (Fig. 68): body shiny black or some specimens distinctly aeneous: low arctic west of Hudson Bay *churchillensis* Wallis
- Larger, L—7.5 to 10.2 mm (\bar{x} > 8.0 mm); metasternal wing broad, WC/WS—2.0 to 3.2 (\bar{x} < 2.6); body broader, L/W—1.82 to 2.03 (\bar{x} < 1.95): aedeagus broad (Figs. 67, 69): body shiny to dull black, never aeneous: low arctic to boreal 6

- 6(5). Aedeagus tapering to a narrow, faintly reflexed apex (Fig. 67); dorsal metatarsal claw with ventral margin sinuate and slightly expanded medially (Fig. 53) *angustior* (Gyllenhal)
- Aedeagus with apex shorter and more bluntly rounded (Fig. 69); dorsal metatarsal claw narrower, ventral margin not expanded medially *picipes* (Kirby)
- 7(1). Sternum 6 with a posteriomedial longitudinal keel 8
- Sternum 6 lacking a medial keel 9
- 8(7). Size small, L—7.8 to 9.1 mm (\bar{x} < 9.0 mm); body narrow, L/W—1.89 to 2.07 (\bar{x} > 1.90); metacoxal plate with striae sparse and lightly impressed *ignarus* LeConte
- Larger, L—8.9 to 11.5 mm (\bar{x} > 9.0 mm); body broader, L/W—1.77 to 1.95 (\bar{x} < 1.90); metacoxal plate densely and conspicuously striolate *biguttulus* Germar
- 9(7). Metasternal wing narrow, WC/WS > 4.5 *oblitus* Sharp
- Metasternal wing broader, WC/WS < 4.5 10
- 10(9). Sternum 6 with posteriomedial area smooth and more or less flattened, laterally with coarse longitudinal or oblique rugae; elytron with many intersections of lines of sculpture each bearing a puncture: paramere lacking adhesive setae: boreal to low arctic 11
- Sternum 6 broadly rounded apically, lacking sublateral rugae; elytron lacking small punctures at intersections of lines of sculpture: paramere with or without adhesive setae: southern boreal and south 12
- 11(10). Sternum 6 with apex truncate or sinuate medially: aedeagus very large with apex reflexed (Fig. 59); prosternal process normal, elongate; metasternal impression reaching level of hind margin of mesocoxae: boreal, transcontinental *discedens* Sharp
- Sternum 6 with apex broadly rounded: aedeagus shorter, apex not reflexed (Fig. 60); prosternal process short, metasternal impression not reaching level of hind margin of mesocoxae: low arctic, west of Hudson Bay *vittiger* (Gyllenhal)
- 12(10). Metasternal wing broad, WC/WS < 2.9: paramere lacking sucker setae on mesal face: aedeagus with a small apical hook (Fig. 61) *fraterculus* LeConte
- Metasternal wing narrower, WC/WS > 2.8: paramere with sucker setae on mesal face: aedeagus with apex simple (Figs. 64, 65) 13
- 13(12). Length 8.7 to 10.0 mm; metasternal wings broad, WC/WS—2.80 to 3.45 *incarinatus* Zimmermann
- Length 9.7 to 11.0 mm; metasternal wings narrower, WC/WS—3.40 to 4.10 *confusus* Aubé

KEY B. FEMALES

1. Metatibia with posterior margin and metatarsomeres 1 to 3 with outer margins bearing long, brown natatorial setae *discedens* Sharp
- Metatibia and metatarsomeres lacking such setae 2
- 2(1). Elytron with intersections of lines of sculpture each with a small puncture: prosternal process short, metasternum with anteromedial impression small and not extending posteriorly to level of hind margin of mesocoxae: low arctic, west of Hudson Bay *vittiger* (Gyllenhal)
- Elytron without evident punctures at intersections of lines of sculpture: prosternal process various but most specimens with metasternal impression extending posteriorly to level of hind margin of mesocoxal cavities 3
- 3(2). Antenna with at least apical flagellomere infusate medially (many specimens with infuscation more expanded on antenna and labial palpus) 4
- Antenna and palpi entirely yellow or pale reddish and devoid of infuscation ... 7

- 4(3). Metatibia with ventral face finely and sparsely punctate on distal $\frac{1}{2}$ to $\frac{2}{3}$, more coarsely punctate at base: size larger, L—9.4 to 11.1 mm: western *quadrimaculatus* Aubé
- Metatibia with coarse punctures along length of ventral face (size and density of punctures may decrease distally on some specimens): smaller, L—7.1 to 10.2 mm: boreal to low arctic 5
- 5(4). Size smaller, L—7.1 to 8.6 mm (population means < 8.0 mm); metasternal wing narrow, WC/WS—2.40 to 3.30 (\bar{x} > 2.60); body narrow, L/W—1.89 to 2.07 (\bar{x} > 1.94): body shiny black or some specimens distinctly aeneous: low arctic west of Hudson Bay *churchillensis* Wallis
- Larger, L—7.5 to 10.2 mm (\bar{x} > 8.0 mm); metasternal wing broader, WC/WS—2.00 to 3.20 (\bar{x} < 2.60); body broader, L/W—1.82 to 2.03 (\bar{x} < 1.95): body shiny to dull black, at most faintly aeneous: low arctic to boreal 6
- 6(5). Gonocoxa, in lateral aspect, with dorsal margin almost straight or only broadly and evenly concave proximad of distal teeth *picipes* (Kirby)
- Gonocoxa with dorsal margin strongly subbasally sinuate or emarginate *angustior* (Gyllenhal)
- 7(3). Metatibia with coarse punctures along length of ventral face (size and density of punctures may decrease distally on some specimens) 8
- Metatibia with apical $\frac{1}{2}$ to $\frac{2}{3}$ of ventral face only finely and sparsely punctate ... 9
- 8(7). Sternum 6 with marginal bead obsolete on outer angle of medial emargination (Fig. 30): elytron with meshes of primary sculpture relatively large and irregular in shape with some fusion of adjacent meshes (Fig. 12): L—10.6 to 12.6 mm ... *pleuriticus* LeConte
- Sternum 6 with marginal bead continuous around lateral angle of medial emargination (Fig. 31): elytron with primary meshes of sculpture smaller and more regular in size and shape (Fig. 13): most specimens with dorsal surface distinctly aeneous: L—9.1 to 11.0 mm *subaeneus* Erichson
- 9(7). Metasternal wing narrow, WC/WS > 4.5 *oblitus* Sharp
- Metasternal wing broader, WC/WS < 4.5 10
- 10(9). Small, L—7.8 to 9.1 mm (\bar{x} < 9.0 mm); elongate, L/W—1.89 to 2.07 (\bar{x} > 1.90): metacoxal plate with striae separate, sparse and lightly impressed: color black with lateral margins piceous or at most narrowly reddish: elytron basomedially with meshes of sculpture small, irregular and not or only slightly longitudinally stretched *ignarus* (LeConte)
- Larger, L—8.4 mm or greater; body broader, L/W—1.73 to 1.98 (\bar{x} < 1.90): metacoxal plate with striae well developed and intersecting: color various: elytral sculpture various 11
- 11(10). Sternum 6 with posteriomarginal emargination deep (Fig. 26): metasternal wings broad, WC/WS—2.3 to 3.0: elytron basomedially with at least some meshes of primary sculpture strongly longitudinally stretched: transcontinental but only common on Great Plains and west *fraterculus* LeConte
- Sternum 6 with medial emargination shallower (Fig. 27): metasternal wing broader, WC/WS—2.55 to 4.10, but if less than 2.80, meshes of elytral sculpture not or only slightly stretched (no meshes more than 3× as long as wide): Rocky Mountains and east but only common east of Great Plains 12
- 12(11). Elytron with meshes of primary sculpture more rounded, few or no meshes more than 3× as long as wide (Fig. 4) *biguttulus* Germar
- Elytron basosuturally with many meshes strongly elongated and more than 3× as long as wide (Figs. 6, 7) 13
- 13(12). Length—8.7 to 10.0 mm: WC/WS—2.80 to 3.40 *incarinatus* Zimmermann
- Length 9.7 to 11.0 mm: WC/WS—3.30 to 4.10 *confusus* Aubé

SPECIES ACCOUNTS

Ilybius discedens Sharp, 1882

Ilybius discedens Sharp 1882:557. (Type area—"Hudsons Bay." Lectotype in BMNH, selected by Larson, 1975.)

Selected reference. Larson 1975:372.

Description. A small species in which males tend to be larger than females: L—7.10 to 9.03 mm; L/W—1.80 to 2.00. Measurements and ratios for selected population samples are given in Table 1.

Color of body dark, mainly black without metallic sheen. Head with frontal spots, labrum and anterior margin of clypeus rufous; lateral margin of pronotum and elytron at most faintly piceous; elytron with sublateral and subapical pale spots evident on most specimens. Palpi entirely rufous. Antenna yellow except apical flagellomere darkened medially and apically. Legs dark rufous to piceous.

Elytron with characteristic sculpture (Fig. 2) of small irregular meshes which bear fine secondary reticulation (may be somewhat effaced basomedially); small punctures present at intersections of lines and a few scattered punctures also present on some meshes.

Prosternum and prosternal process with ventral margin concave medially between procoxae in lateral aspect, medial convexity of prosternum somewhat swollen or inflated anteriorly; prosternal process strongly tectiform and not explanate basally, basal bead of more or less uniform width behind procoxae; apex acuminate apically but short. Metasternal impression attaining level of hind margin of mesocoxal cavities. Metasternal wings relatively narrow (WC/WS—2.85 to 4.11) but with a relatively high degree of intraspecific variation.

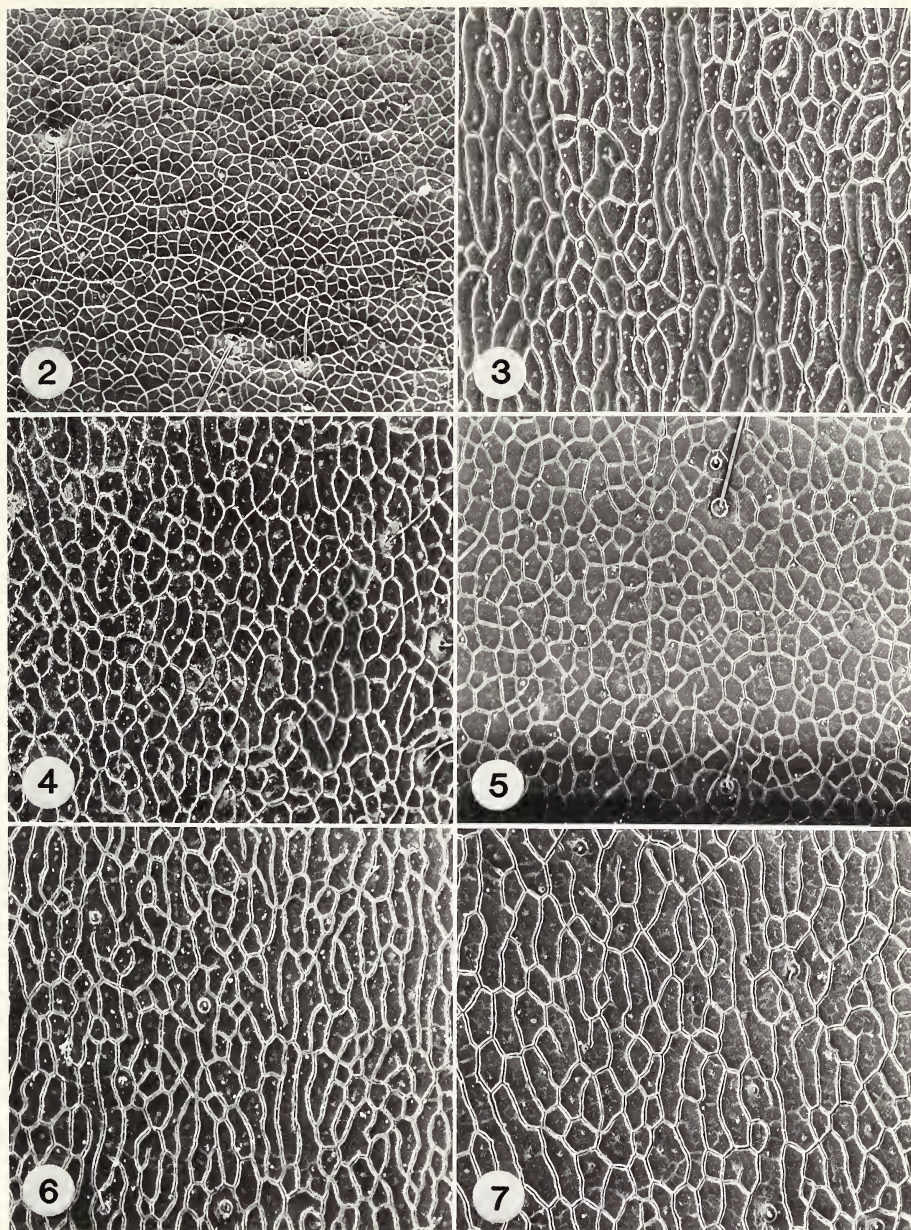
Metacoxal plate with striae shallow, sparse and more or less separated; shallow punctures present but somewhat obscured by microreticulation. Metacoxal lines strong, slightly sinuate anteriorly, traceable to metasternum.

Metafemur with ventral face finely punctate, striae absent. Metatibia with a few coarse punctures basally on ventral face, otherwise impunctate or with only a few very fine punctures. Longer metatibial spur subequal in length to metatarsomere 1. Metatarsomere 1 lacking ventrolateral setae.

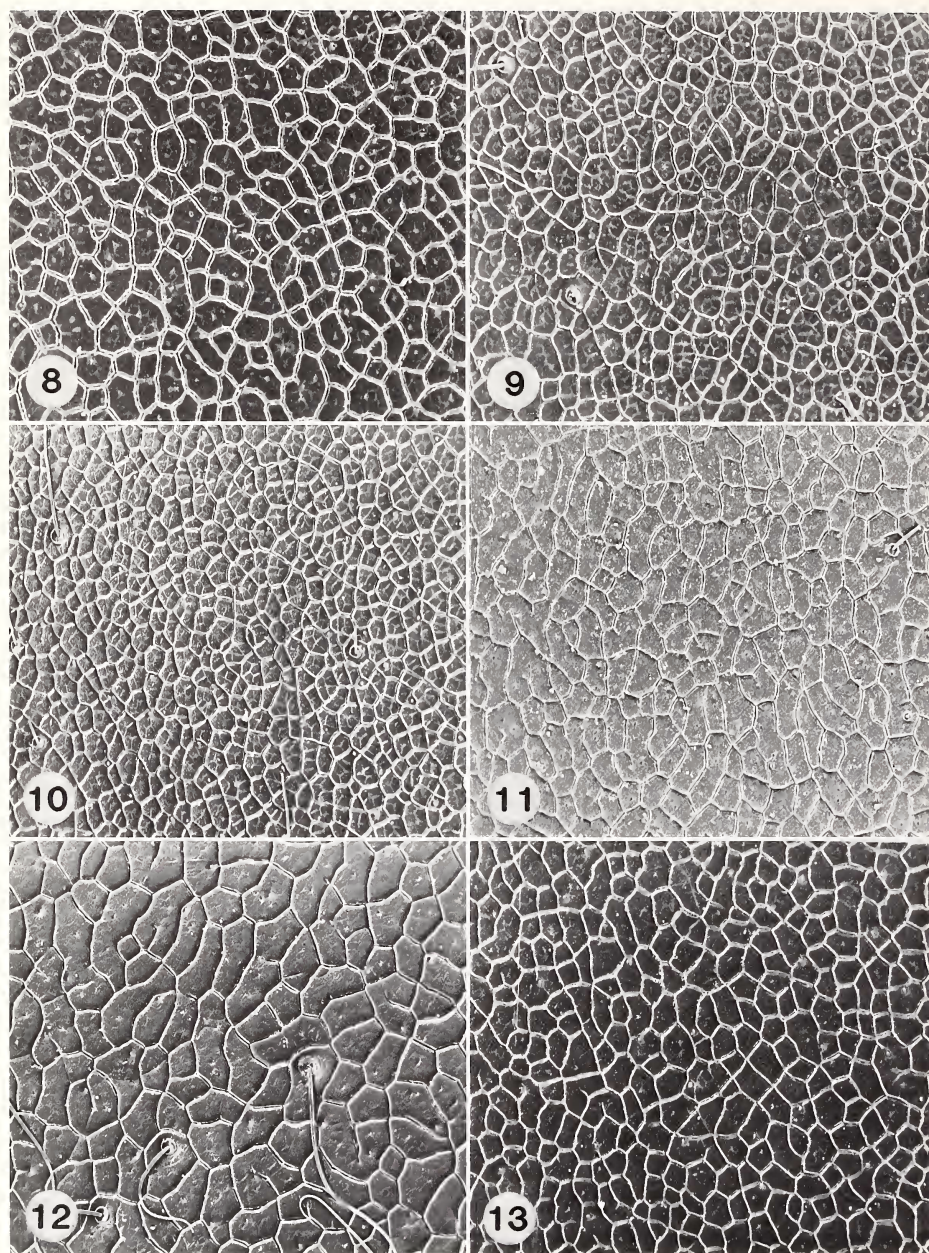
Table 1. Measurements and ratios of selected population samples of *Ilybius discedens* Sharp.

Locality	N	Length L	Maximum width W	L/W	WC/WS
Newfoundland, pooled, ♂	20	8.51 (0.24) 8.00–9.03	4.41 (0.12) 4.22–4.74	1.93 (0.03) 1.89–2.00	3.48 (0.19) 3.03–3.78
Newfoundland, pooled, ♀	20	8.14 (0.26) 7.55–8.50	4.20 (0.12) 4.00–4.37	1.94 (0.03) 1.89–1.98	3.57 (0.17) 3.27–4.00
S. Labrador, ♂	20	8.13 (0.36) 7.55–8.73	4.27 (0.21) 3.92–4.59	1.91 (0.03) 1.85–1.98	3.54 (0.19) 3.21–4.00
S. Labrador, ♀	20	7.58 (0.23) 7.10–8.14	3.97 (0.16) 3.63–4.29	1.91 (0.04) 1.80–2.00	3.66 (0.22) 3.27–4.11
N. Alberta	20	8.20 (0.32) 7.68–9.04	4.32 (0.18) 4.08–4.80	1.90 (0.03) 1.85–1.96	3.18 (0.17)* 2.85–3.54

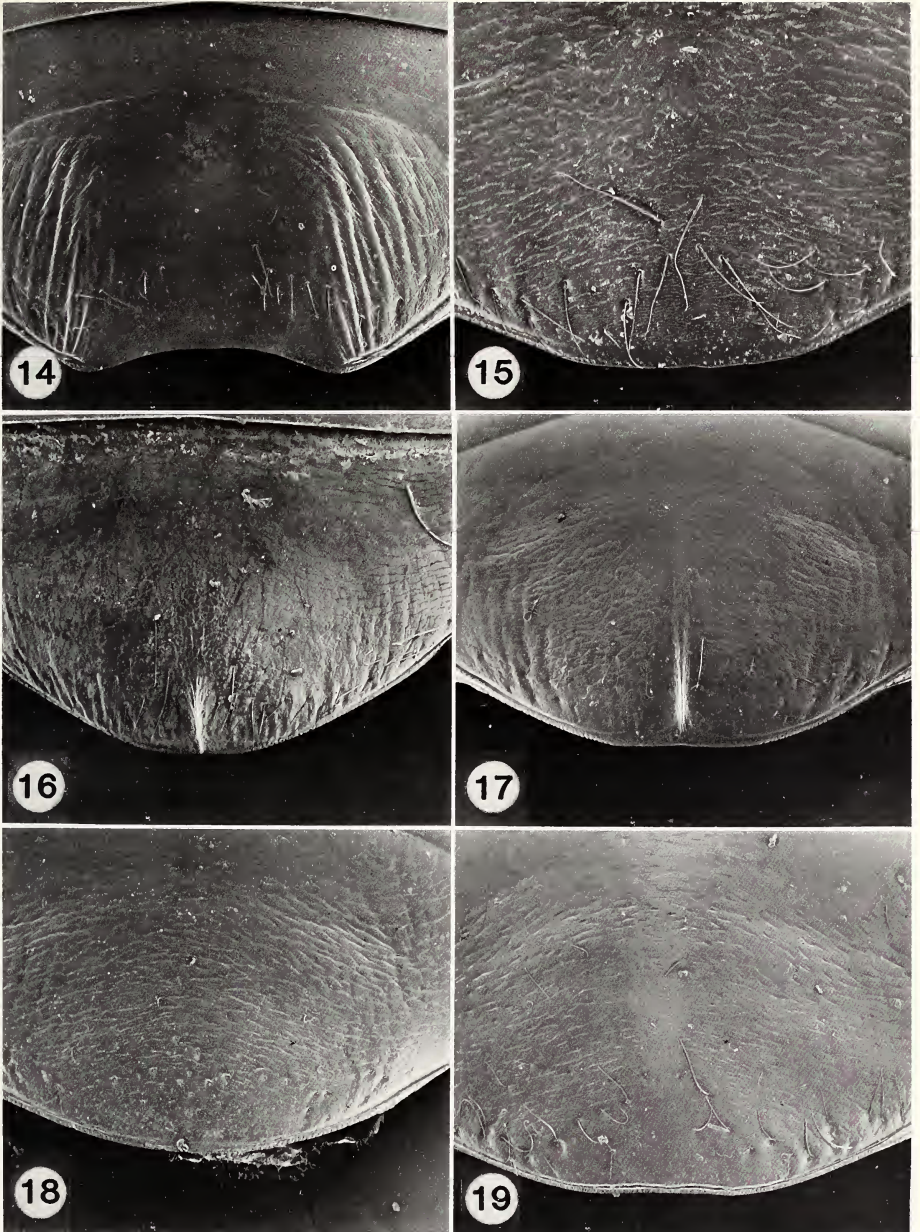
* From Larson (1975), WS includes width of coxal rim.



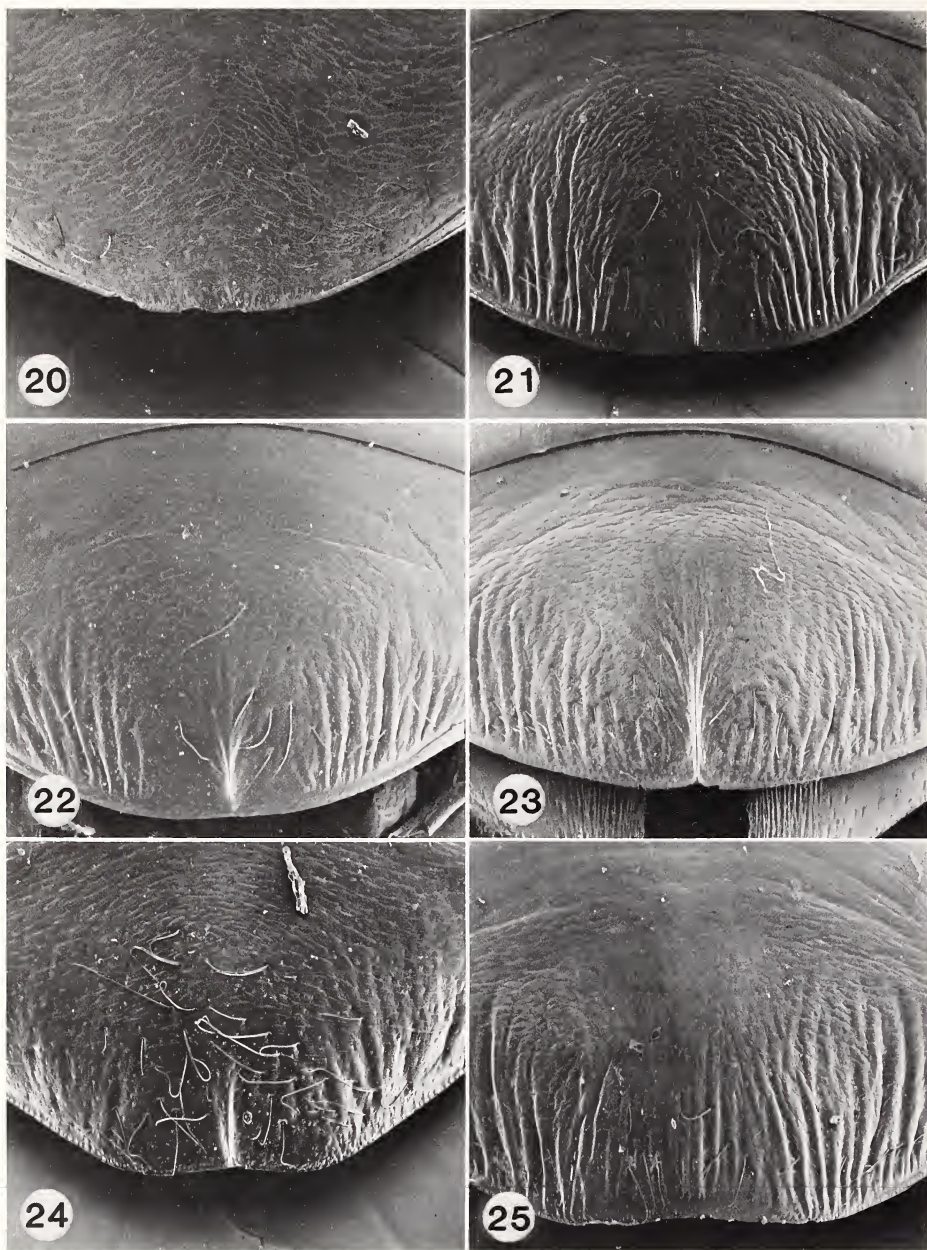
Figs. 2-7. Elytral microsculpture, basomedial area of disc. 2. *I. discedens*. 3. *I. fraterculus*. 4. *I. biguttulus*. 5. *I. ignarus*. 6. *I. incarinatus*. 7. *I. confusus*. Magnification $\times 150$.



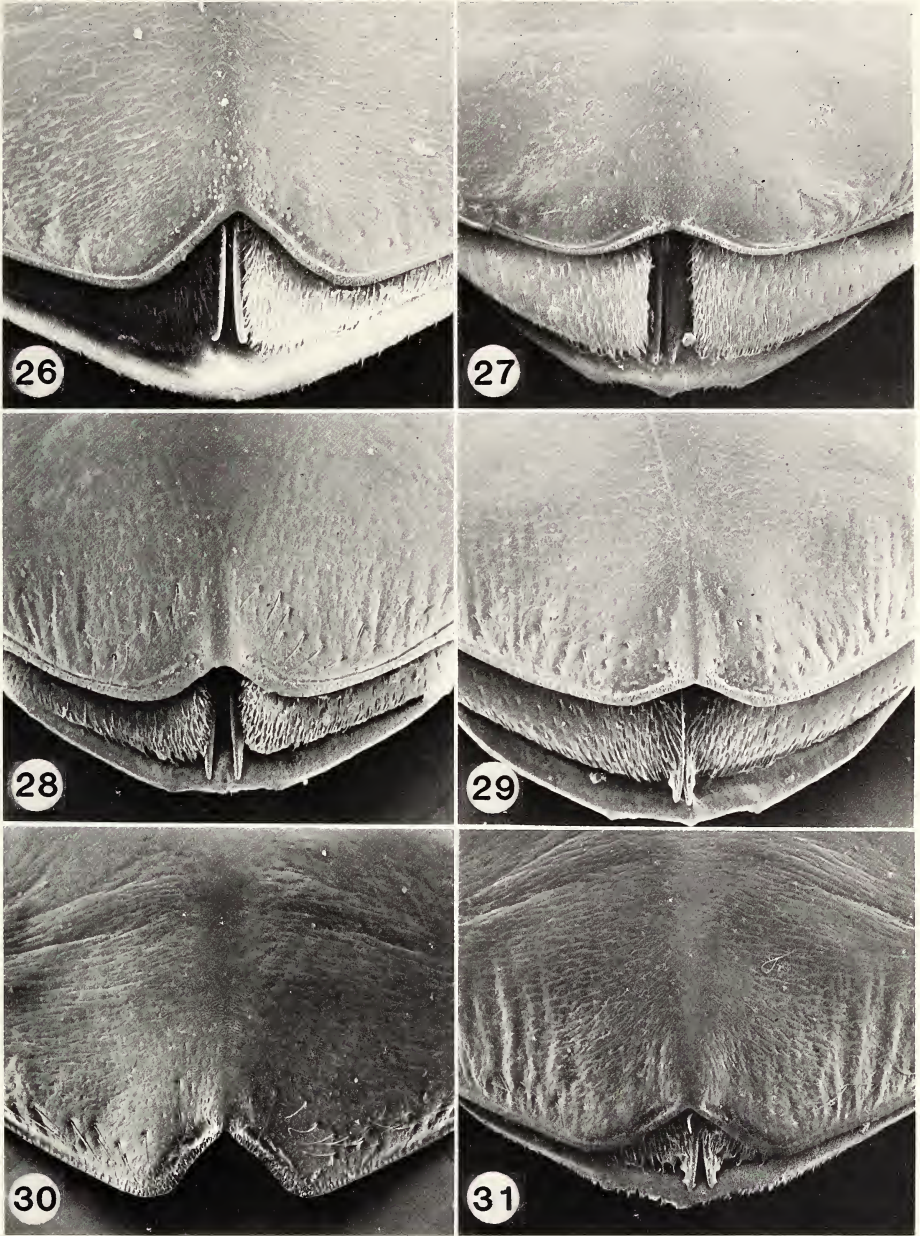
Figs. 8–13. Elytral microsculpture, basomedial area of disc. 8. *I. oblitus*. 9. *I. angustior*. 10. *I. picipes*. 11. *I. quadrimaculatus*. 12. *I. pleuriticus*. 13. *I. subaeneus*. Magnification $\times 150$.



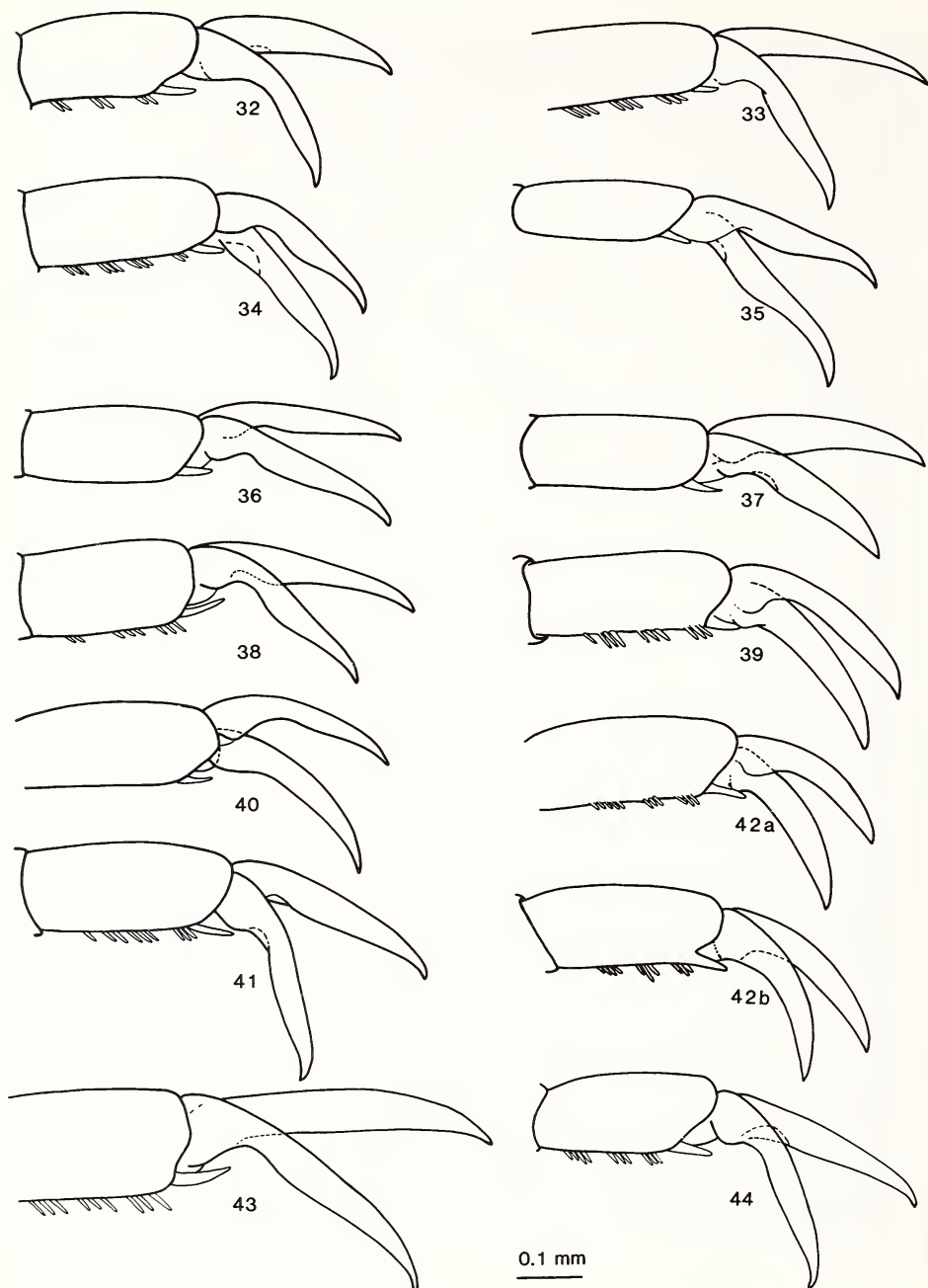
Figs. 14–19. Male sternum 6, ventral aspect. 14. *I. discedens*. 15. *I. fraterculus*. 16. *I. biguttulus*. 17. *I. ignarus*. 18. *I. incarinatus*. 19. *I. confusus*. Magnification $\times 50$.



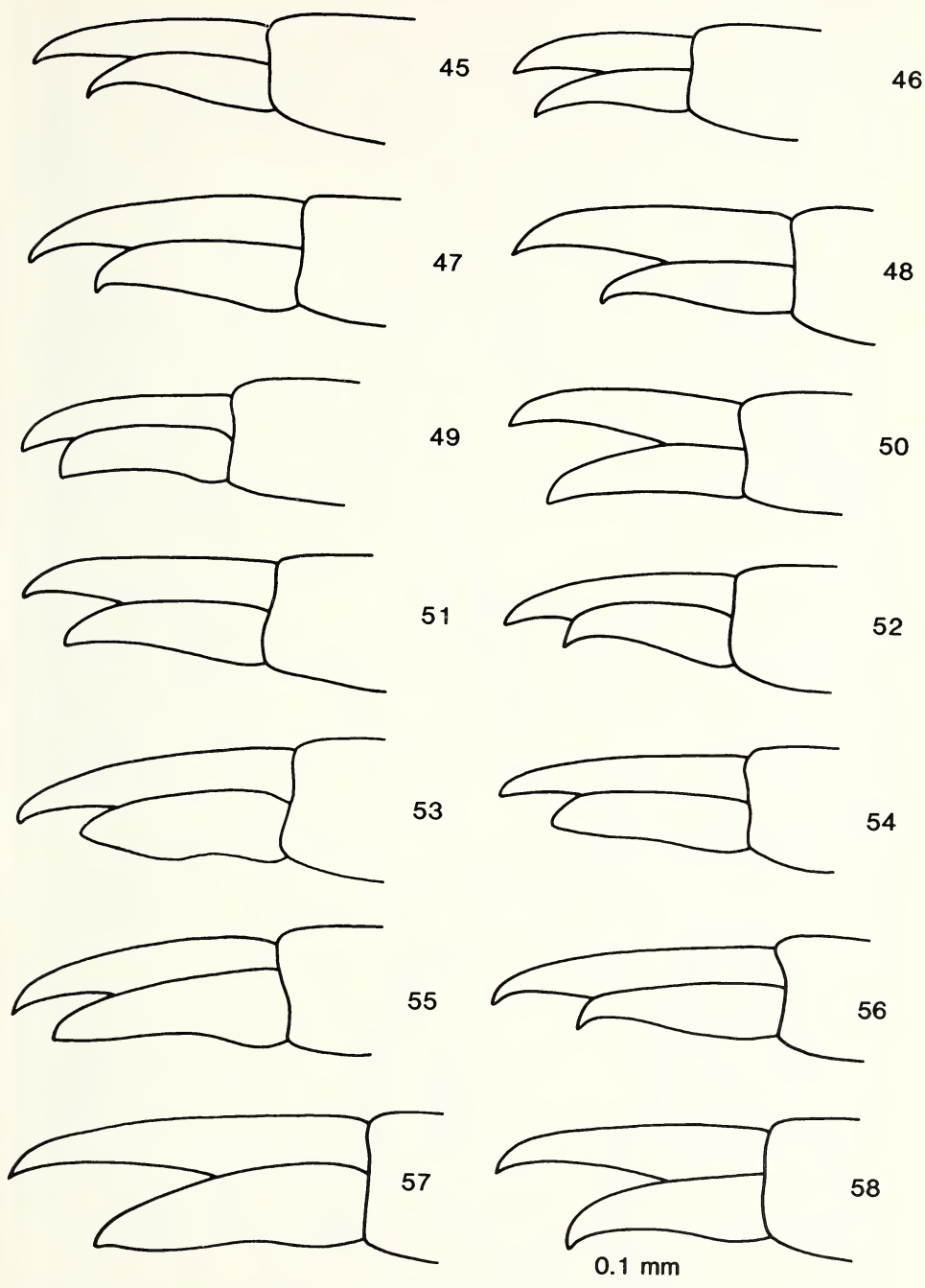
Figs. 20–25. Male sternum 6, ventral aspect. 20. *I. oblitus*. 21. *I. angustior*. 22. *I. picipes*. 23. *I. quadrimaculatus*. 24. *I. pleuriticus*. 25. *I. subaeneus*. Magnification $\times 50$.



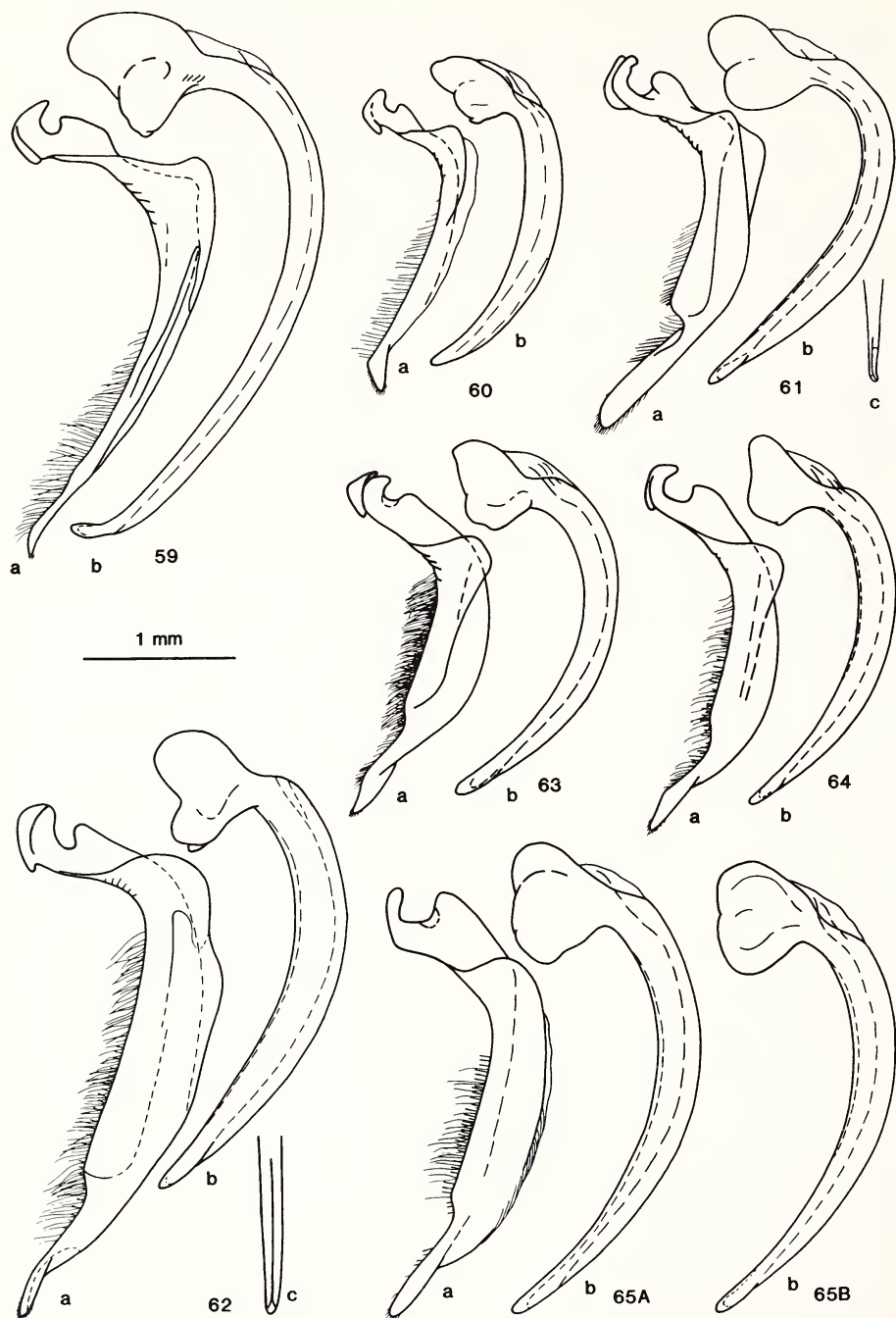
Figs. 26-31. Female sternum 6, ventral aspect. 26. *I. fraterculus*. 27. *I. confusus*. 28. *I. angustior*. 29. *I. quadrimaculatus*. 30. *I. pleuriticus*. 31. *I. subaeneus*. Magnification $\times 50$.



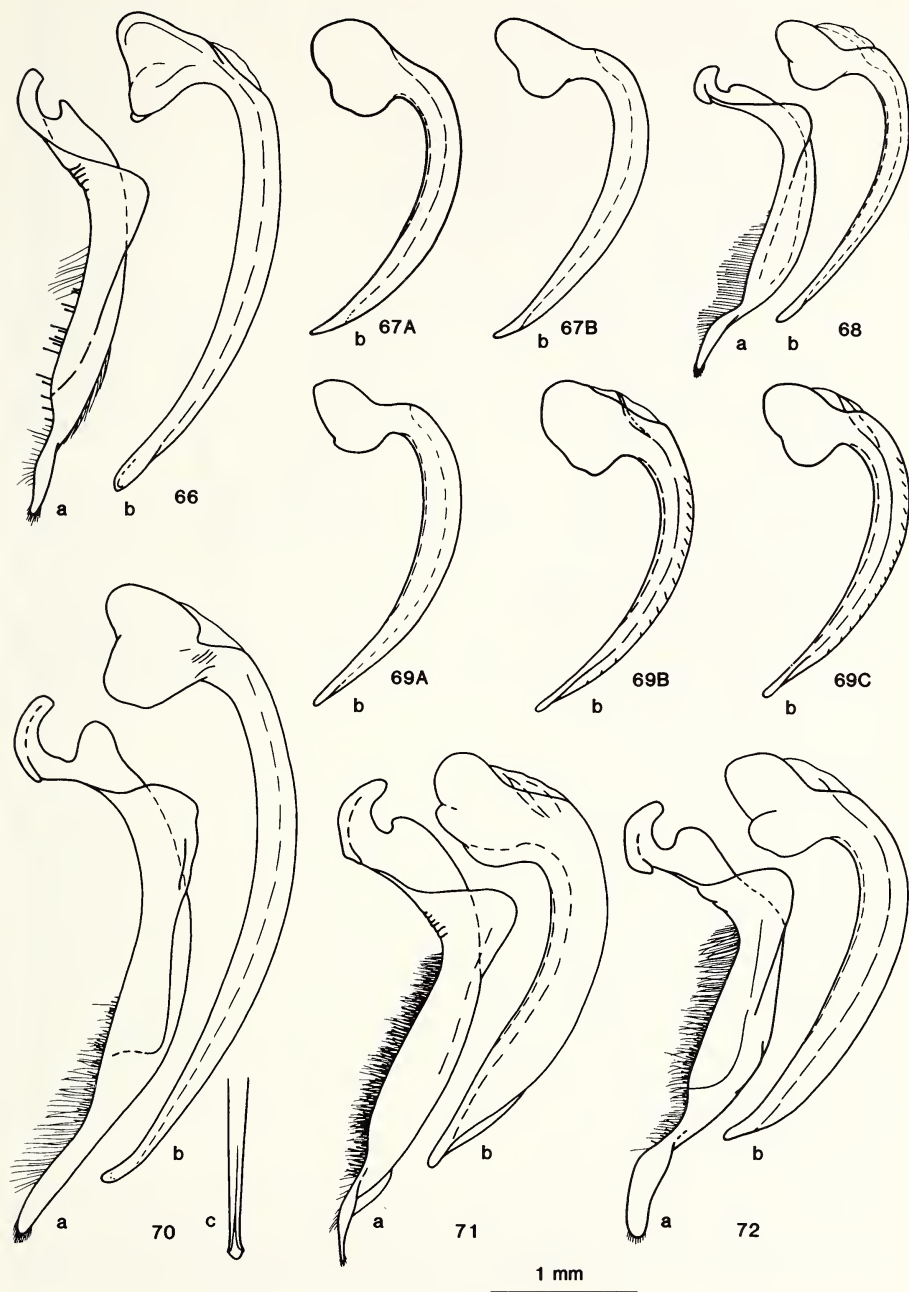
Figs. 32-44. Male, left protarsal claws, anterior aspect. 32. *I. discedens*. 33. *I. fraterculus*. 34. *I. biguttulus*. 35. *I. ignarus*. 36. *I. incarinatus*. 37. *I. confusus*. 38. *I. oblitus*. 39. *I. angustior*. 40. *I. churchillensis*. 41. *I. quadrimaculatus*. 42. *I. picipes*, a—Alaska, b—Ontario. 43. *I. pleuriticus*. 44. *I. subaeneus*.



Figs. 45–58. Male, left metatarsal claws, dorsal aspect. 45. *I. discedens*. 46. *I. vittiger*. 47. *I. fraterculus*. 48. *I. biguttulus*. 49. *I. ignarus*. 50. *I. incarinatus*. 51. *I. confusus*. 52. *I. oblitus*. 53. *I. angustior*. 54. *I. churchillensis*. 55. *I. picipes*. 56. *I. quadrimaculatus*. 57. *I. pleuriticus*. 58. *I. subaeneus*.



Figs. 59-65. Male genitalia: a—paramere, lateral aspect; b—aedeagus, lateral aspect; c—aedeagus apex, ventral aspect. 59. *I. discedens*. 60. *I. vittiger*. 61. *I. fraterculus*. 62. *I. biguttulus*. 63. *I. ignarus*. 64. *I. incarinatus*. 65. *I. confusus*, A—paratype of *I. denikei*, B—Specimen from Massachusetts.



Figs. 66–72. Male genitalia: a—paramere, lateral aspect; b—aedeagus, lateral aspect; c—aedeagus apex, ventral aspect. 66. *I. oblitus*. 67. *I. angustior*. 68. *I. churchillensis*. 69. *I. picipes*, A—specimen from Alaska, B—Ontario, C—Manitoba. 70. *I. quadrimaculatus*. 71. *I. pleuriticus*. 72. *I. subaeneus*.

MALE: Protarsal claws (Fig. 32) slender, especially posterior claw which is abruptly narrowed about middle. Metacoxae with posteriomedial keel absent or at most weakly developed. Metatarsomeres lacking a dorsolateral ridge or bead. Metatarsal claws (Fig. 45) with dorsal claw smoothly arcuate. Sternum 6 (Fig. 14) with apex broadly truncate or shallowly bisinuate: flat and smooth posteriomedially and longitudinally striate laterally, lateral bead absent across medial flattened area. Subgenital plate truncate apically, striate laterally but largely smooth medially: lateral sclerites longitudinally strigate. Male genitalia (Fig. 59) with paramere slender, setose on mesal margin but lacking sucker setae; aedeagus very elongate, longer than paramere, apex broadened and reflexed ventrally.

FEMALE: Secondary reticulation of elytron more strongly developed than on male, elytra of most specimens slightly duller than those of male. Metatibia with mesal margin and metatarsomeres along outer margin bearing elongate brown natatorial setae. Sternum 6 with lateral angles of apical emargination broadly rounded and semicircular, emargination compressed in posterior aspect, medially sternum raised into a low crest in lateral aspect with ventroapical margin right angled or produced as a small spine.

Variation. This species differs from other North American *Ilybius* in that the average size of males is greater than that of females (Table 1). This sexual size difference is especially pronounced in Labrador while in western North America the sexual size disparity is less noticeable.

The range of variation in the ratio WC/WS is large but does not show a geographical pattern. At least part of this large variation is an artifact created by expressing the character as a ratio, for a given numerical variation in a small denominator (WS) will produce a greater spread in values of the ratio than will the same amount of variation in a larger denominator.

Nomenclature. Data on the lectotype was given by Larson (1975).

Classification notes. This species occupies a rather isolated position within the genus because of the possession of several peculiar characters. The occurrence of natatorial setae on the metatibia and outer margins of the metatarsomeres of the female is unique within the genus and even among the members of the tribe Agabini with which I am familiar. The aedeagus is also distinctive, being exceptionally elongate relative to the body length and with the apex flattened and reflexed. On the other hand, the species possesses several plesiotypic characters, namely: simple parameres which lack sucker setae; and elytral sculpture with well developed punctures located at intersections of lines of primary sculpture. Larson and Roughley (1983) associated *I. discedens* with *I. vittiger* principally on these very characters, while recognizing that the two species differ in many other features. It appears more probable that the relationship between *I. discedens* and *I. vittiger* is not close and is based primarily on synplesiotypic features.

Ecology. This is one of the most characteristic water beetle species of boreal peatlands (Larson, 1985). The beetles occur in small, moss-ringed pools, often where the water is cold to the touch. The life history has not been investigated but because adults are common in the spring and teneral beetles are found primarily in July and August, it appears as though adult overwintering occurs regularly. Overwintering *Ilybius* larvae, presumably of *I. discedens*, have also been observed in small peat pools in Newfoundland. I have not seen records of flight.



Map 1. Collection localities for *Ilybius discedens*.

Distribution. *Ilybius discedens* has a wide distribution in the northern boreal portion of the nearctic region. The range extends from Newfoundland to western Alaska and from the northern limit of trees south into the northeastern United States (Map 1).

Ilybius vittiger (Gyllenhal, 1827)

Dytiscus vittiger Gyllenhal 1827:379. (Type area—"Laponiae borealis." Type in Museum of Zoology, Uppsala, Sweden. Type not seen.)

Selected references. Larson and Roughley, 1983. Nilsson, 1983.

Description. The habitus of this species is somewhat unusual for a member of *Ilybius*: the body is relatively depressed and broadly oval in outline, in this respect resembling a member of the genus *Agabus*. Size small, L—6.8 to 7.85 mm, L/W—1.75 to 1.93.

Color of body piceous to black dorsomedially, without metallic reflection. Head with labrum, anterior margin of clypeus and frontal spots, rufous to piceous. Pronotum narrowly piceous laterally. Elytron with lateral margin, or on some specimens entire disc, piceous. Antenna rufous or some specimens with apical antennomere faintly infusate. Palpi rufous. Legs rufous to rufopiceous.

Elytron with primary meshes of sculpture large, of very irregular shape and without distinct longitudinal stretching. Intersections of lines with small punctures, also small punctures located in many meshes. Secondary microreticulation present but on many specimens effaced basally.

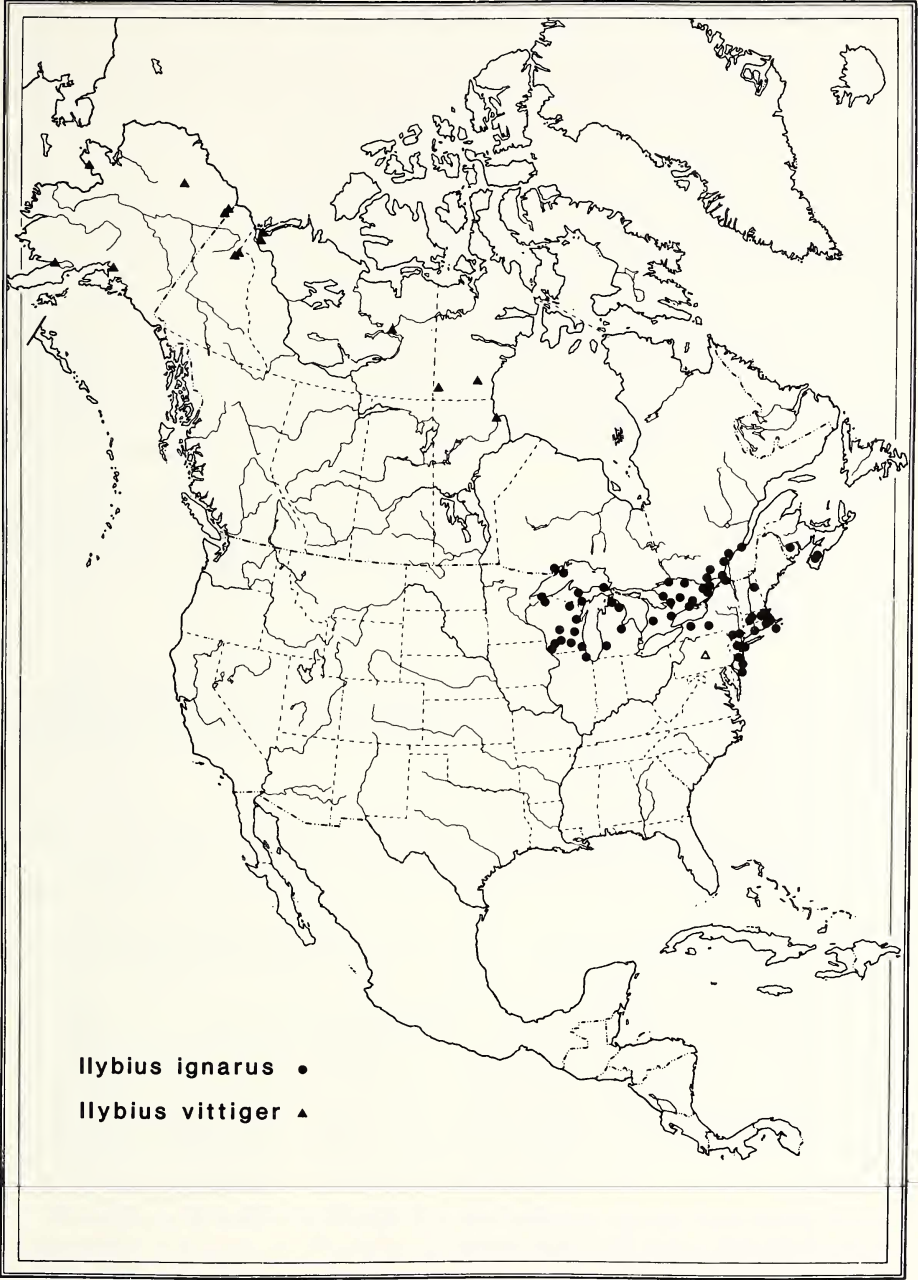
Prosternal process relatively short, tectiform: lateral bead not inflated behind procoxae. Metasternal impression short, its apex not attaining level of hind margin of mesocoxal cavities. Metasternal wings moderately narrow, WC/WS—2.75 to 3.67.

Metacoxal plate with striae lacking or weakly developed: its surface microreticulate and with poorly defined transverse rugae. Metacoxal lines traceable to metasternum.

Hind legs relatively narrow. Metafemur with small punctures but lacking striae. Metabibia with irregular coarse punctures on ventrolateral face, these punctures distributed along entire length of tibia or on many specimens becoming smaller or disappearing on distal third to half. Metatibial spurs subequal in length to metatarsomere 1. Metatarsomere 1 with one or more coarse setae along ventrolateral margin of most specimens. Metatarsal claws with only a slight disparity in size; dorsal claw with apex more arcuate than ventral claw, its apex not reaching as far distad as apex of ventral claw.

MALE: Protarsomeres 1 to 3 only slightly broadened, with a very small group of golden setae on ventroapical portion of each: protarsal claws slender, anterior and posterior each slightly sinuate ventrally. Metacoxae with a very small longitudinal keel along posterior portion of medial line. Metatarsomeres 1 to 3 lacking a dorso-lateral bead. Metatarsal claws as in Figure 46. Sternum 6 with apex broadly rounded or slightly emarginate medially: ventral surface smooth medially with lateral longitudinal rugae: lateral bead absent or only weakly defined across apex. Subgenital plate broad and slightly emarginate apically, it and lateral plates longitudinally rugose. Genitalia (Fig. 60) with paramere slender, lacking adhesive setae along mesal face. Aedeagus subequal in length to paramere, simple in form with apex narrowly rounded.

FEMALE: Metatibia along mesal margin and metatarsomeres along outer margin



Map 2. North American collection localities for *Ilybius vittiger* and *I. ignarus*. Open triangle represents a state record for *I. ignarus*.

lacking natatorial setae. Sternum 6 with a narrow medioapical emargination: medially with a prominent rounded ventral knob; laterally to knob with a few scattered coarse setiferous punctures, smaller micropunctures and, on most specimens, an area of prominent transverse or oblique microrugae: lateral bead complete along hind margin of sternum except where narrowly broken on crest of knob.

Variation. No pattern of geographic variation has been detected and North American specimens are similar to those from the western palaearctic.

Classification notes. The systematic position of this species has been discussed by Larson and Roughley (1983) and its placement in *Ilybius* also confirmed by Nilsson (1983). The species was postulated as being the sister species of *I. discedens* but the association proposed was based on plesiotypic characters (see below).

Ecology. Nilsson (1983) described the larva and discussed the ecology. The species occurs in the northern boreal and arctic portions of Fennoscandia where it inhabits small bog pools with sparse vegetation. It occurs in similar habitats in North America except it is known only from localities north of the tree line. Nilsson reports that this is an autumn-breeder with overwintering larvae. There are no North American records of flight.

Distribution. This species is holarctic in distribution, occurring across the northern boreal and low arctic portion of the Palaearctic region and on the arctic mainland of western North America east to the eastern Northwest Territories and northern Manitoba (Map 2).

Ilybius fraterculus LeConte, 1862

Ilybius fraterculus LeConte 1862:521. Type specimen: female, in MCZ, labelled: (yellow disc, two sides cut)/Type 6042/*C. fraterculus* Lec./*biguttulus*?. Type locality was given as North Red River.

Selected reference. Larson 1975:373–4.

Description. Size moderate, 9.3–11.4 mm; body moderately elongate, L/W—1.74–2.01. Measurements on selected population samples are presented in Table 2.

Dorsal surface piceous to black, with a faint cupreous sheen on some specimens.

Table 2. Measurements and ratios for selected population samples of *Ilybius fraterculus* LeConte.

Locality	N	Length L	Maximum width W	L/W	WC/WS
S. Alberta	20	10.22 (0.22)	5.53 (0.12)	1.85 (0.03)	2.42 (0.06)*
		9.76–10.64	5.36–5.76	1.74–1.91	2.32–2.55
S. Manitoba	20	9.94 (0.35)	5.37 (0.18)	1.85 (0.03)	2.60 (0.08)
		9.32–10.51	5.11–5.70	1.80–1.89	2.50–2.87
N. Dakota	17	10.22 (0.27)	5.50 (0.12)	1.86 (0.04)	2.57 (0.10)
		9.77–10.65	5.25–5.70	1.78–1.92	2.43–2.84
Arizona, California, Utah	7	10.51 (0.35)	—	—	2.75 (0.12)
		10.06–11.17			2.54–2.95
California, Modoc Co.	27	10.62 (0.35)	5.62 (0.20)	1.89 (0.04)	2.71 (0.12)
		9.77–11.40	5.25–5.99	1.80–2.01	2.51–2.97

* From Larson (1975), WS includes width of coxal rim.

Head with frontal spots, anterior margin of clypeus and labrum, rufous: antenna and palpi entirely yellow. Lateral margins of pronotum and elytra broadly reddish: epipleuron rufous. Ventral surface and legs, rufous to piceous.

Pronotum with sculpture consisting of irregular, somewhat rounded meshes over most of disc; however, mediolaterally and sublaterally some meshes are elongated and subparallel. Elytron (Fig. 3) with lines deep, meshes relatively coarse: basally and along suture many meshes narrow and longitudinally stretched with many meshes 3 or more times as long as broad: laterally and apically meshes more rounded in outline and without a definite pattern of orientation: meshes with secondary sculpture obsolete over most of disc and coherent only at extreme apex. Intersections of lines lacking punctures.

Prosternal process elongate, acute apically: lateral bead of moderate width behind procoxae and not evidently inflated, in ventral aspect apex of process more or less evenly narrowed apically from level of termination of lateral bead: in lateral aspect ventral surface of process more or less straight. Metasternum with anteriomedial impression extending posteriorly to level of hind margin of mesocoxae. Metasternal wings broad, WC/WS—2.32 to 2.97.

Metacoxal plate with reticulation distinct but fine, subshiny: striae deep but short, little sinuate and for the most part separate.

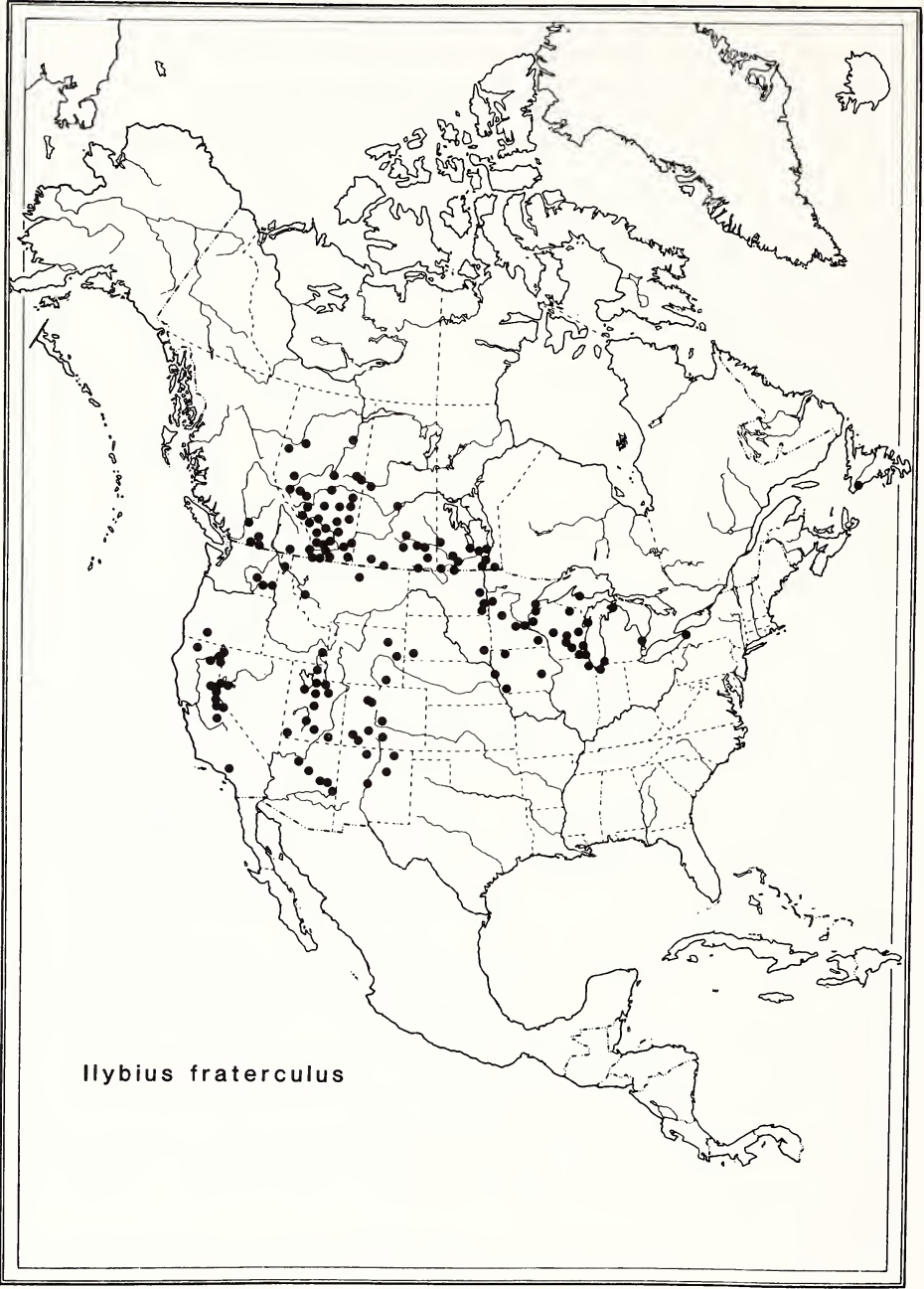
Metafemur finely but distinctly punctate, punctures rounded or a few slightly elongate and forming fine striae. Metafemur with coarse punctation of ventral face restricted to basal third, distal two thirds sparsely and finely punctate. Metatarsomere 1 lacking ventrolateral setae.

MALE: Posterior protarsal claw slightly shorter and narrower than anterior, sinuate ventrally with a shallow ventral basal emargination (Fig. 33). Metatarsus with dorsal claw arcuate apically (Fig. 47). Sternum 6 (Fig. 15) unmodified, lacking rugae and median keel, lateral bead obsolete or faintly traceable medially. Subgenital plate broad apically, subtruncate or shallowly emarginate apically; it and lateral sclerites strigate. Paramere with inner face lacking sucker hairs but with patches of stiff setae near medial shoulder and at base of apical piece: inner basal face broadly sclerotized, lateral face with sclerotized area narrow, shoulder very prominent. Aedeagus with apex bent in a short but distinct hook.

FEMALE: Metatibia and lateral margin of metatarsomeres lacking natatorial setae. Sternum 6 (Fig. 26) with a deep V-shaped posteriomedial emargination: sides of emargination little pinched, lateral angles obtuse but prominent and relatively narrowly rounded, completely margined.

Variation. Specimens from the southern portion of the range (Arizona, Utah and California) tend to be slightly larger and have a larger WC/WS ratio than specimens from the northern Great Plains, but there is considerable overlap in the range of values between these populations (Table 2). No other characters have been noted as varying geographically.

Nomenclatural notes. The female type has relatively narrow metasternal wings for a specimen of this species (WC/WS—2.92) but it does fall within the observed range. I have assigned it to this species rather than *I. biguttulus* because of its large size, somewhat stretched elytral meshes (although this is not strongly developed), short, more or less isolated striae of the metacoxa, and the relatively deeply emarginate sternum 6.



Map 3. Collection localities for *Ilybius fraterculus*.

Classification notes. The parameres have a well developed subapical shoulder but unlike all other species with parameres of this configuration, sucker setae are absent from the mesal face. A group of stout setae are present mesally near the shoulder and they may represent modified sucker setae or be derived from normal vestiture which has become stouter in localized areas. Because of similarity in general paramere form with species with sucker setae, I interpret their absence as loss and not as a plesiotypic state. The absence from males of both rugae on sternum 6 and beading of the metatarsomeres is shared with members of the *I. biguttulus* group as is the reduced metafemoral punctation and the tendency of meshes of the primary elytral sculpture to become longitudinally stretched.

Ecology. This species occurs primarily in grassland ponds, usually where the water is sunwarmed but where emergent vegetation is abundant. Larson (1985) noted that of the western species of *Ilybius* this is the most adapted to warm, temporary ponds. Gordon and Post (1965) found this species to be attracted to ultraviolet light in large numbers in North Dakota.

Distribution. Collection records extend across the continent at mid latitudes, but the species is common only from the western Great Lakes area and west (Map 3). The single record from Newfoundland is most unexpected and probably represents a vagrant as the species is known to fly readily.

Ilybius biguttulus (Germar, 1824)

Dytiscus biguttulus Germar 1824:29. Type are: North America (type not seen, type repository not located).

Ilybius laramaeus LeConte 1859a:4. Lectotype (here designated), male in MCZ labelled: green disc/Type 6073/*C. laramaeus* LeC. **NEW SYNONYMY** (see Nomenclatural Notes).

Selected references. Sharp 1882:558; Leng 1920:80; Fall 1927:283, Wallis 1939:197–8.

Description. Size moderate, 8.4 to 11.4 mm, body relatively broadly oval, L/W—1.77 to 1.98. Measurements for selected population samples are given in Table 3.

Color dorsally piceous to black except anterior margin of head, frontal spots and lateral margins of pronotum and elytra reddish to piceous: antenna and palpi yellow to light red, without apical infuscation; legs and epipleuron reddish.

Elytron with meshes of sculpture of small to moderate size and irregular shape (Fig. 4), some males and most females with meshes on basosutural portion of disc somewhat longitudinally stretched but generally length of longest meshes not more than 3 times their width (on some specimens a few meshes 4 or 5× as long as wide have been observed); secondary reticulation effaced or faint basally, evident on apical third to half. Intersections of lines not punctate.

Prosternal process elongate, narrow and acuminate apically: process with lateral bead relatively broad between and behind procoxae; in ventral aspect apex of process abruptly narrowed at level of termination of broadened portion of lateral bead; process in lateral aspect with ventral margin more or less straight or slightly convex. Metasternal impression extending beyond level of hind margin of mesocoxal cavities. Metasternal wings broad, WC/WS—2.55 to 3.32.

Metacoxal plates with striae well impressed, dense, elongate and with various

Table 3. Measurements and ratios for selection population samples of *Ilybius biguttulus* Germar.

Locality	N	Length L	Maximum width W	L/W	WC/WS
Newfoundland, pooled	27	10.12 (0.46)	5.50 (0.27)	1.84 (0.05)	2.87 (0.11)
		9.18–11.40	5.03–5.99	1.77–1.94	2.64–3.06
Nova Scotia, Sable I.	10	9.35 (0.26)	5.13 (0.13)	1.82 (0.03)	3.00 (0.13)
		9.03–9.77	4.88–5.33	1.77–1.86	2.77–3.24
Quebec, Kazubazua	20	9.60 (0.30)	5.14 (0.18)	1.87 (0.03)	2.88 (0.12)
		8.88–10.06	4.74–5.48	1.81–1.94	2.55–3.08
Maryland, Baltimore	20	9.40 (0.39)	5.10 (0.21)	1.84 (0.03)	2.92 (0.10)
		8.43–10.06	4.59–5.48	1.79–1.91	2.76–3.12
Eastern Kansas	19	9.99 (0.25)	5.48 (0.10)	1.83 (0.03)	2.95 (0.11)
		9.62–10.51	5.33–5.62	1.78–1.88	2.76–3.14
Wyoming, pooled	14	10.29 (0.37)	5.44 (0.21)	1.89 (0.21)	2.89 (0.17)
		9.47–10.73	5.03–5.70	1.78–1.98	2.70–3.28
Colorado, Trinidad	15	9.87 (0.28)	5.35 (0.16)	1.85 (0.03)	3.11 (0.10)
		9.47–10.51	5.11–5.70	1.81–1.93	2.93–3.29
Pooled Colorado, New Mexico, Utah	10	10.13 (0.43)	5.49 (0.24)	1.85 (0.03)	3.04 (0.04)
		9.47–10.95	5.10–5.92	1.81–1.92	2.80–3.32

degrees of interconnection: transverse rugae shallow but evident. Metacoxal lines evenly diverging anteriorly, not attaining metasternal suture.

Metafemur very finely punctate, without elongated punctures or striae. Metatibia with ventral surface finely and sparsely punctate medially except for coarse punctures on basal third and along hind margin: longer metatibial spur slightly longer than metatarsomere 1. Metatarsomere 1 lacking mediodorsal and ventrolateral setae.

MALE: Posterior protarsal claw slightly shorter, narrower and more strongly sinuate ventrally than anterior: both claws with a ventrobasal impression, best developed on posterior claw (Fig. 34). Metacoxae with a small longitudinal keel on posterior region of medial line. Metatarsomeres lacking externodorsal bead: dorsal metatarsal claw tapered and shortly arcuate at apex (Fig. 48). Sternum 6 (Fig. 16) smooth or with a few shallow longitudinal rugae along posterior margin, setiferous punctures evident: a short but distinct posteriomedial longitudinal keel present: lateral bead of sternum obsolete medially near keel. Subgenital plate broad apically with a shallow medial emargination, it and lateral plates with coarse longitudinal striae. Male genitalia (Fig. 62) with paramere bearing sucker hairs on ventral face, aedeagus simple, subequal in length to paramere.

FEMALE: Metatibia with inner margin and metatarsomeres with outer margin lacking natatorial setae. Sternum 6 with posteriomedial emargination of moderate size, lateral angles broadly obtuse and rounded, lateral bead disappearing on angle and internally replaced by a dense marginal array of small punctures: in posterior aspect sides of emargination not or only slightly pinched and middle only slightly raised as a knob.

Variation. This species varies geographically in elytral sculpture, size, relative width, and in the WC/WS ratio. However, the amount of variation is slight with a

great deal of overlap in character states, even between widely separated populations. No pattern of concordance in variation in two or more characters was observed, therefore there are no grounds for recognizing infraspecific groupings of populations.

The largest specimens were from the extremes of the range, Newfoundland and the western Great Plains and Rocky Mountain States. Specimens from Wyoming are on average slightly narrower than specimens from most other populations, but the difference is not statistically significant. The range in values for WC/WS is as great between many adjacent populations as it is between populations from extremes of the range.

A generally useful character for recognizing female specimens of *I. biguttulus* is the shape of the primary meshes of the elytral sculpture. Meshes on the basomedial portion of the elytra of most specimens are short and only slightly elongated while on similar species, namely *I. fraterculus*, *I. incarinatus* and *I. confusus*, at least some meshes are very elongate. However, longitudinally stretched meshes do occur on some female specimens of *I. biguttulus*. This condition was observed among many specimens from northern Quebec, but it also appears on a few specimens from all parts of the range making this character somewhat unreliable for identification purposes, especially when only single specimens are available.

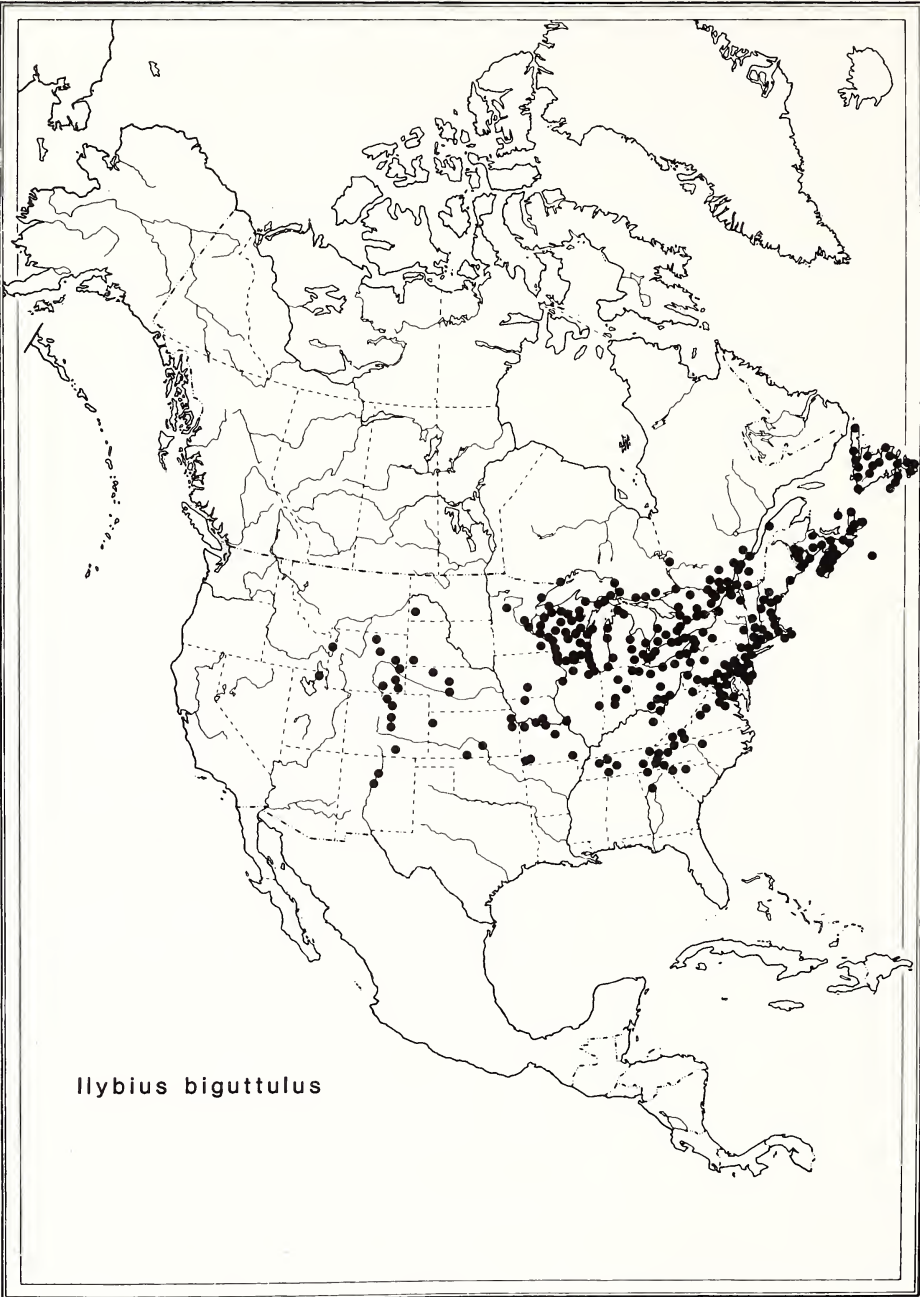
Nomenclatural notes. I have not seen the type specimen of *I. biguttulus* (Germar). However, my concept of the species is consistent with that of the LeConte collection, Crotch (1873), Fall (1927) and Wallis (1939).

The validity of the name *I. laramaeus* LeConte was doubted by Fall (1927), but Fall apparently vacillated in his recognition of the species (Wallis, 1939). Wallis (1939) resurrected *I. laramaeus* relying primarily on its narrower form and larger size (in contrast Fall (1927) noted the length of *I. laramaeus* was less than that of *I. biguttulus*) for its separation from *I. biguttulus*, and also providing a number of other minor differences in male pro- and metatarsal claws, and shape of sternum 6 of both sexes. Measurements do not substantiate the size and shape differences (see above and Table 3), nor am I able to support recognition of *I. laramaeus* on other characters; thus I agree with Fall's suggested synonymy.

LeConte (1859b:509) and Fall (1927) both considered *Colymbetes fenestralis* Say (1823:95–96) to be a senior synonym of *I. biguttulus* Germar. This cannot be demonstrated conclusively as Say's types are lost. Say's description offers several important clues as to the identity of his species, namely:

- "antennae and palpi piceous"—The antennae and palpi are not piceous in *I. biguttulus*.
- "sternum acutely carinated"—The acutely carinated sternum may refer to the presence of a carina on abdominal sternum 6 of the male but it is more likely a reference to the shape of the prosternum which Say referred to as the sternum in descriptions of other species in the same paper.
- "It delights in mirey forest springs"—*I. biguttulus* does occur among emergent vegetation in forest springs but the description suggests cold water and peaty habitats, a more usual habitat for *I. angustior* or *I. picipes*.

On the whole, the name probably refers to the species, *I. picipes* Kirby and is senior to *picipes* Kirby. However, because of the tenuous evidence I consider *I. fenestralis* a nomen dubium.



Map 4. Collection localities for *Ilybius biguttulus*.

Table 4. Measurements and ratios for selected population samples of *Ilybius ignarus* LeConte.

Locality	N	Length L	Maximum width W	L/W	WC/WS
Ontario & Quebec	14	8.58 (0.33)	4.40 (0.18)	1.95 (0.06)	3.01 (0.10)
		7.80–9.03	4.14–4.67	1.89–2.07	2.85–3.24
Michigan	12	8.55 (0.36)	4.43 (0.20)	1.93 (0.03)	3.07 (0.08)
		7.84–9.03	4.07–4.66	1.90–1.98	2.97–3.23

Classification notes. The male genitalia, including aedeagal and paramere features, are similar among *I. biguttulus*, *I. ignarus*, *I. oblitus*, *I. confusus* and *I. incarinatus*. Other characters shared by these species include: reduced punctation of the metatibia, lack of bead on dorsolateral margins of male metatarsomeres, lack of rugae on male sternum 6, and relatively shallowly emarginate female sternum 6. *I. oblitus* is distinctive due to the very narrow metasternal wing, deeply impressed primary sculpture of the elytron, and short prosternal process. *I. confusus* and *I. incarinatus* are characterized by elongate meshes of the primary elytral sculpture and lack of a carina on male sternum 6. *I. biguttulus* and *I. ignarus* are very similar but *I. biguttulus* is larger, broader, with coarser elytral sculpture, metacoxal plates with striae better developed and male sternum 6 with carina shorter. The overall close similarity of *I. biguttulus* and *I. ignarus* suggests these are sister species which in turn have a common ancestor with the *I. confusus*-*I. incarinatus* ancestor.

Ecology. This species occurs in small lentic habitats, where the water is usually sunwarmed and the vegetation is dense. In Newfoundland, where the *Ilybius* fauna is rich (7 species known), this species is found in the warmest, most nutrient-rich habitats occupied by any of the species. I have seen many records of flight between 30 May and 26 July, as well as single records for 20 August and 1 September.

Distribution. *Ilybius biguttulus* has a wide distribution in eastern north America, from the southern boreal zone of Newfoundland and Quebec, south to northern Georgia. It is also found in the Rocky Mountain states, from Wyoming to New Mexico and Utah, as well as sparingly across the south-central Great Plains (Map 4).

Ilybius ignarus (LeConte, 1862)

Colymbetes ignarus LeConte 1862:521. Lectotype.—here selected, male in MCZ labelled as follows: pale blue disc/"type 6071"/"*C. ignarus* LeC." Type locality not stated but pale blue disc is LeConte's color code for Lake Superior, Canada, and north.

Selected references. Sharp 1882:554; Leng 1920:80; Fall 1927:283; Wallis 1939:197.

Description. This is a small (length 7.8 to 9.1 mm), elongate (L/W—1.89 to 2.07), black species. Measurements for two population samples are given in Table 4.

Color of body black dorsally except frontal spots, anterior margin of clypeus and lateral margins of pronotum and elytron dark rufous to piceous: antenna and palpi entirely pale, without infuscation: venter mainly black with epipleuron and legs dark reddish.

Elytron (Fig. 5) with sculpture consisting of small meshes of irregular size and

shape which either show no tendency of longitudinal stretching, or basosuturally a few meshes slightly elongated: secondary sculpture obsolete basally but evident apically: intersections of lines without punctures.

Prosternal process elongate, apically acuminate: lateral bead broadened between procoxae; in ventral aspect process evidently constricted at level of termination of thickened portion of lateral bead then more or less evenly narrowed towards apex. Metasternal impression well developed and extending posteriorly to level of hind margin of mesocoxal cavities. Metasternal wings somewhat narrower than in *I. biguttulus*, WC/WS—2.85 to 3.24.

Metacoxal plates with microreticulation relatively lightly impressed, surface shiny: striae sparse, shallow, short and more or less isolated; sparse punctation distinct. Metacoxal lines not reaching metasternal suture.

Metafemur with ventral face finely punctate, nonstrigate. Metatibia with ventral face finely and sparsely punctate except for coarse punctures at base and along hind margin. Longer metatibial spur slightly longer than metatarsomere 1. Metatarsomere 1 lacking dorsal and ventral coarse spines.

MALE: Anterior and posterior protarsal claws (Fig. 35) similar in shape, shallowly but evidently sinuate ventrally, the posterior claw most distinctly so. Metacoxae with a small longitudinal keel on posterior portion of medial line. Metatarsomeres lacking bead on outer dorsal margin: dorsal metatarsal claw (Fig. 49) slender, its apex narrowly rounded. Sternum 6 (Fig. 17) with posterior margin smooth or faintly rugose, setiferous punctures evident; with a low medial longitudinal keel which on most specimens is at least faintly traceable along midline of posterior half of sternite: lateral bead well developed and continuous along hind margin to medial keel. Subgenital plate with apex broad and shallowly emarginate, it and lateral plates coarsely strigate. Male genitalia (Fig. 63) with paramere bearing sucker hairs of irregular length along inner face: aedeagus simple.

FEMALE: Metatibia with inner margin and metatarsomeres along outer margin lacking natatorial setae. Sternum 6 with apical emargination shallow, lateral margins of emargination appearing pinched in posterior aspect so that sternum at middle is produced as a short knob or ridge: lateral bead complete around lateral angles of emargination.

Variation. No geographical or appreciable intrapopulation variation has been noted.

Nomenclatural notes. The LeConte Collection (MCZ) contains 9 specimens under the name *I. ignarus*. In addition to the lectotype, specimens are from Escabanba, Michigan (2); White Fish Point, Lake Superior (5); and a female specimen of the *I. angustior* complex bearing a pale blue disc. The lectotype bears the label "C. ignarus LeC.," presumably in LeConte's handwriting. It is teneral and brown, not black, in color.

Classification notes. *Ilybius ignarus* is similar to *I. biguttulus*, differing mainly in size, shape, and sculpture of elytra and metacoxal plates (see notes under *I. biguttulus*).

Ecology. Adults have been collected from peatland pools. Mr. C. Chantal (in litt.) has reported specimens collected in bottle traps situated in open water areas of acidic peat bogs. Specimens have been collected at light between 29 June and 25 July, and 14 September.

Distribution. The distribution is rather limited, with collection records occurring primarily in the northern Appalachian region and adjacent boreal areas (Map 2).

Table 5. Measurements and ratios for selected population samples of *Ilybius incarinatus* Zimmermann.

Locality	N	Length L	Maximum width W	L/W	WC/WS
Ontario & Quebec	7	9.29 (0.39)	5.21 (0.19)	1.78 (0.05)	3.09 (0.13)
		8.73–9.92	5.03–5.55	1.73–1.86	2.84–3.22
Massachusetts, pooled	37	9.51 (0.30)	5.27 (0.17)	1.80 (0.05)	3.08 (0.12)
		8.88–10.14	4.88–5.70	1.70–1.95	2.78–3.39
New York and Connecticut, pooled	6	9.60 (0.17)	5.41 (0.06)	1.77 (0.03)	3.20 (0.11)
		9.40–9.77	5.33–5.48	1.73–1.81	3.05–3.29
Illinois, pooled	15	9.24 (0.34)	5.12 (0.18)	1.81 (0.03)	3.07 (0.15)
		8.58–9.84	4.81–5.48	1.75–1.86	2.79–3.31

Ilybius incarinatus Zimmermann, 1928

Ilybius incarinatus Zimmermann 1928:181–2. Lectotype (here designated)—male in ZSM, labelled—“Nord-Amerique”/“♂”/blue disc “type”/Lectotype, *Ilybius incarinatus* Zimmermann, des. D. Larson.” Type locality given as Glauco, Illinois.

Selected reference. Wallis 1939:198.

Description. Size moderate (L—8.5 to 10.1 mm), body relatively broad (L/W—1.70 to 1.95). Measurements and ratios for selected population samples are presented in Table 5 and Figure 73. This species is very similar to *I. confusus* but is smaller and darker in color.

Head red, palest anteriorly and darkened between eyes and along posterior margin; antenna and palpi entirely pale. Pronotum piceous medially, lateral margins broadly reddish. Elytra piceous to black medially, lateral margins lateral of submedial spot, reddish, disc either gradually darkened mesad or some specimens with transition to dark color of disc relatively abrupt; epipleuron red. Ventral surface and legs red to piceous.

Elytron basosuturally (Fig. 6) with many narrow, elongate, parallel meshes interspersed with shorter smaller meshes, many meshes 5× or more as long as wide: laterally and posteriorly meshes less evidently stretched and more rounded or irregular in shape. Meshes smaller and more regular than in *I. confusus*, with fewer laterally confluent meshes.

Prosternal process elongate and acuminate: marginal bead somewhat inflated between procoxae; in ventral aspect apex relatively abruptly constricted distad of broadened portion of lateral bead; in lateral aspect apical portion deflected dorsad and somewhat out of plane of basal portion of process, or some specimens with ventral margin broadly arched. Metasternum with anteriomedial impression reaching level of hind margin of mesocoxal cavities. Metasternal wings moderately broad, WC/WS—2.7 to 3.5.

Metacoxal plates with striae fine, elongate, somewhat sinuate and variously branched or interconnected, especially posteriorly; striae longer and better developed than on *I. confusus*. Metacoxal lines not attaining metasternal suture.

Metafemur finely punctate, with a few very fine striae present posteriomedially. Metatibia with ventral face finely punctate except for coarse punctures at base and

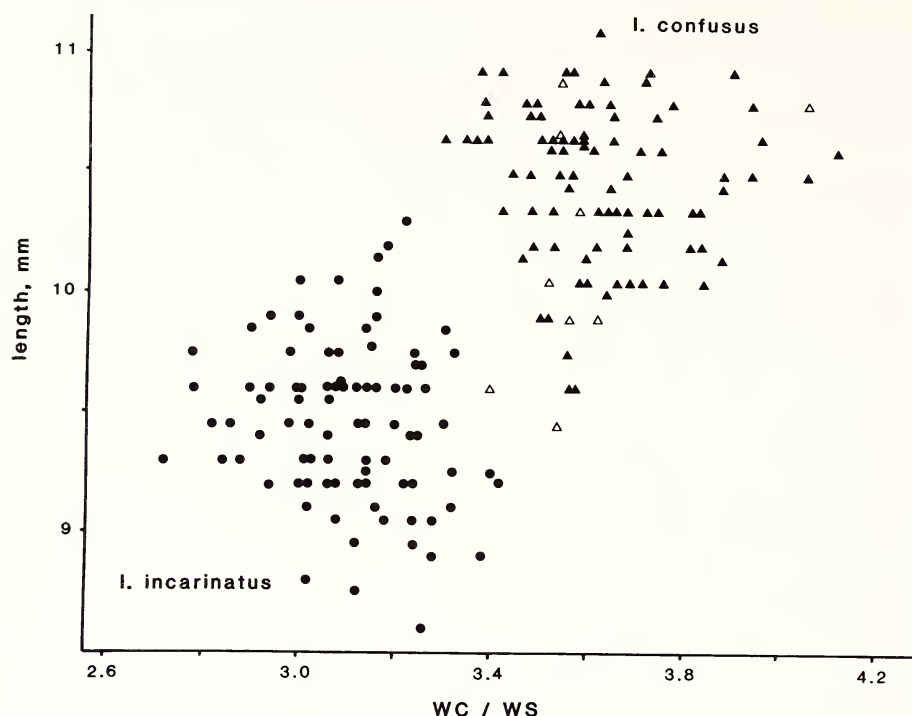


Fig. 73. Scatter diagram of length versus WS/WC for specimens of *I. confusus* (closed triangles) and *I. incarinatus* (closed circles). Open triangles represent specimens from Washington, D.C., of which the two specimens intermediate between *I. confusus* and *I. incarinatus* are best assigned to *I. incarinatus*, the remainder belong to *I. confusus*.

along hind margin. Longer metatibial spur longer than metatarsomere 1. Metatarsomere 1 lacking dorsal and ventral longitudinal spines.

MALE: Protarsal claws (Fig. 36) similar in shape but posterior claw slightly shorter than anterior, ventrally each claw slightly sinuate and emarginate basally. Metacoxae with a small keel on posterior portion of medial line. Metatarsomeres lacking dorsoexternal bead. Dorsal metatarsal claw (Fig. 50) narrow, subparallel and broadly rounded to ventroapical point. Sternum 6 unmodified, broadly rounded or slightly truncate apically, completely margined laterally; surface lacking rugae and posteromedial keel. Subgenital plate broad apically, it and lateral plates strigate. Genitalia (Fig. 64) with paramere and aedeagus of *biguttulus* type.

FEMALE: Metatibia with internal margin and metatarsomeres with outer margin lacking natatorial setae. Sternum 6 with apical emargination shallow, in posterior aspect sides slightly compressed with middle produced as a short rounded knob; marginal bead complete except at crest of medial knob.

Variation. See Classification Notes.

Nomenclatural notes. A. Zimmermann described this species from two specimens, a male and a female. He referred to the specimens as type and cotype but did not



Map 5. Collection localities for *Ilybius incarinatus* and *I. churchillensis*.

distinguish which was type. Each specimen bears a blue disc with type written on it. I selected the male specimen as the lectotype.

Classification notes. Specimens of *I. incarinatus* are very similar to those of *I. confusus*, differing mainly quantitatively in character states rather than through possession of any unique feature. For example, the aedeagus of *I. incarinatus* is shorter than that of *I. confusus* but aedeagal length is correlated with, and bears the same relation to, body length in both species ($r = 0.93$) indicating that specimens of *I. confusus* are larger than those of *I. incarinatus*. The two best characters for discriminating between the species are body length and the ratio WC/WS (Fig. 73). Specimens segregate into two well defined groups with no geographical pattern of variation in either character except population samples from Washington, D.C., and New Jersey contain a few specimens that are difficult to place. These intermediate specimens appear to be large specimens of *I. incarinatus* as definite specimens of *I. confusus* from the area fall well within the range of measurements of *I. confusus*. The shape of the prosternal process of these intermediate specimens is similar to that of *I. incarinatus*, supporting their assignment to this species.

Because the two forms occupy approximately the same geographical area and because almost all specimens fall clearly into one group or the other, recognition of two species seems well justified. It is possible that hybridization may occur in Washington, D.C., and southern New Jersey. In all other regions the two species are distinct. There is no evidence of geographical variation nor do specimens of either species from regions from which only one species is known show any different degree of variation than those from areas where both occur sympatrically.

Ecology. Nothing is known about the habitat of this species. Specimens have been collected at light from June 12 to 23 in Massachusetts, Quebec and Washington, D.C.

Distribution. This species occurs in the region around the Great Lakes and south to Washington, D.C., and Tennessee (Map 5).

Ilybius confusus Aubé, 1838

Ilybius confusus Aubé 1838:280. Type area: United States, type not located.

Ilybius denikei Wallis 1933:271. Holotype: male in CNC, CNC type no. 5650, type locality-Ingolf, Ontario. **NEW SYNONYMY.**

Selected references. Sharp 1882:559; Leng 1920:80; Fall 1927:284-5; Wallis 1939:199.

Description. This is a moderately large (length 9.7 to 11.0 mm), broad (L/W—1.73 to 1.91) species. Measurements and ratios for selected population samples are presented in Table 6.

Color various, body rufous to piceous dorsally with lateral margins broadly paler reddish: red lateral margins gradually darkened mesad on disc or some specimens with body laterad of sublateral elytral vittae abruptly paler: elytron with subapical vitta present as a small triangular or crescentic spot, sublateral vitta various in size ranging from a small oval spot subequal in size to subapical vitta to a long line about half length of elytron. Antenna and palpi pale, without infuscation. Ventral surface and legs red to piceous.

Elytron with sculpture various, basosuturally (Fig. 7) most specimens with some

Table 6. Measurements and ratios for selected population samples of *Ilybius confusus* Aubé.

Locality	N	Length L	Maximum width W	L/W	WC/WS
Ontario, Ingolf	20	10.35 (0.31)	5.80 (0.14)	1.78 (0.03)	3.67 (0.14)
		9.77–10.95	5.55–6.07	1.73–1.81	3.41–4.07
Massachusetts, pooled	28	10.57 (0.23)	5.87 (0.11)	1.80 (0.05)	3.55 (0.12)
		10.06–10.95	5.62–6.07	1.68–1.91	3.37–3.84
New York, pooled	12	10.67 (0.29)	5.91 (0.18)	1.80 (0.04)	3.57 (0.18)
		9.92–10.95	5.48–6.07	1.75–1.86	3.33–3.97
Washington, D.C.*	10	10.13 (0.52)	5.62 (0.31)	1.80 (0.02)	3.59 (0.18)
		9.47–10.88	5.18–6.07	1.78–1.86	3.41–4.06
New Jersey, pooled	5	10.30 (0.60)	5.80 (0.24)	1.77 (0.05)	3.46 (0.20)
		9.47–10.95	5.48–6.07	1.73–1.85	3.14–3.68

* Sample contains some specimens intermediate between *I. confusus* and *I. incarinatus* (see Fig. 73).

meshes of primary sculpture longitudinally stretched and with a few meshes $5\times$ or more as long as wide: meshes coarser than in *I. incarinatus*, not so regular in form with more lateral fusion of adjacent meshes to give many meshes of very irregular shape on basosutural portion of disc (a few specimens have been seen in which the sculpture is similar to that of *I. biguttulus* with meshes small, rounded and not especially stretched or laterally fused).

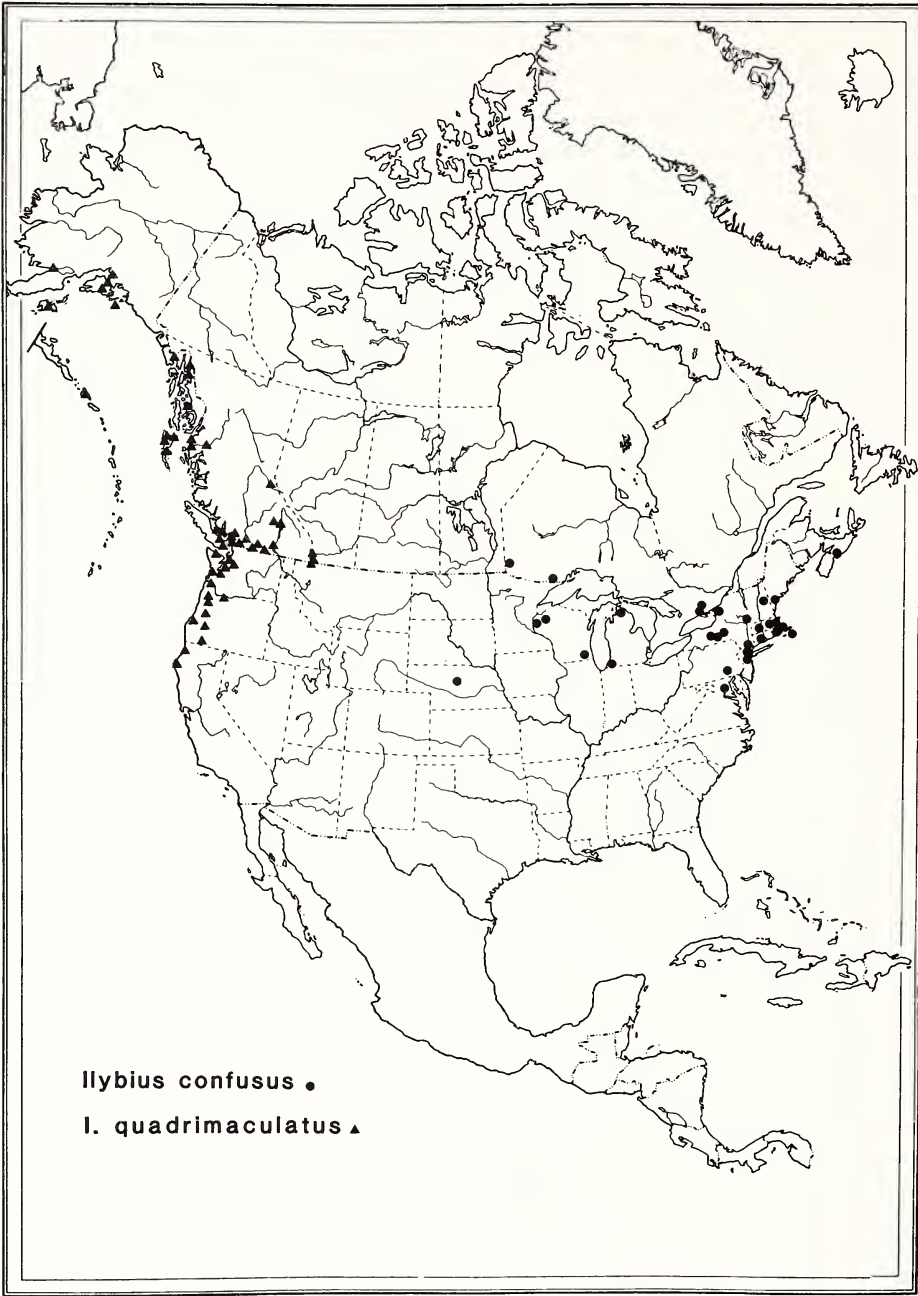
Prosternal process elongate and acuminate apically: lateral bead evidently broadened between procoxae; in ventral aspect apex more or less evenly tapered distally from level of termination of broadened portion of lateral bead, apex more evenly narrowed than in *I. incarinatus*: in lateral aspect, ventral margin straight or only slightly convex. Metasternal impression extended posteriorly to level of hind margin of mesocoxal cavities. Metasternal wing narrow, WC/WS—3.3 to 4.1.

Metacoxal plate with dense subparallel striae but striae short and more or less separate. Metacoxal lines not reaching metasternal suture.

Metafemur finely and sparsely punctate, without or with only very faint striae near posterior margin. Metatibia with ventral face finely punctate medially and distally or with a sparse row of slightly larger punctures along mid longitudinal region; coarser punctures present at base and paralleling inner margin. Longer metatibial spur longer than metatarsomere 1. Metatarsomere 1 lacking ventrolateral coarse setae.

MALE: Protarsal claws (Fig. 37) each with a small ventrobasal emargination. Medial metacoxal line with a faint keel near posterior end. Metatarsomeres lacking dorsolateral bead. Metatarsal claws (Fig. 51) with dorsal claw slightly arcuate, narrowing gradually towards apex. Sternum 6 (Fig. 19) with apex more or less truncate, marginal bead complete: ventral surface smooth and without longitudinal rugae or posteromedial keel. Subgenital plate with apex broad, emarginate medially, it and lateral plates longitudinally strigate. Male genitalia (Fig. 65) with parameres and aedeagus of *biguttulus* type, sucker hairs present on medial face of paramere.

FEMALE: Metatibia along internal margin and metatarsomeres externally lacking natatorial setae. Sternum 6 (Fig. 27) shallowly emarginate apically, lateral angles of emargination very broadly rounded and with a complete marginal bead: in posterior



Map 6. Collection localities for *Ilybius confusus* and *I. quadrimaculatus*.

aspect sides of emargination compressed and middle of emargination acutely produced.

Variation. Specimens of *I. confusus* vary somewhat in size and in the width of the metasternal wing, but specimens are for the most part separated from those of *I. incarinatus* by distinct gaps in these measurements (Fig. 73, see discussion under *I. incarinatus*). This variation is mainly intrapopulation.

Specimens from western Ontario are conspicuously paler than those from other localities. They have the heads and sides of the body broadly reddish and the sub-lateral vitta of the elytron is broad and elongate (one quarter to half the length of the elytron). Wallis described this pale form as *I. denikei*. As I have not discovered any characters other than color for separating *I. denikei* from other specimens of *I. confusus*, I consider it a junior synonym of *I. confusus*. Specimens of *I. subaeneus* from certain localities in western Ontario are also exceptionally pale so that there seems to be some environmental factor in the area promoting the development of paler color in certain species of *Ilybius*. Wallis stated that the type series of *I. denikei* was collected on a sandy lake shore. Often water beetles occurring in exposed sites or on pale mineral substrates are paler or more strongly patterned than usual (Young, 1960), and this may be the explanation for the unusual color of the *I. denikei* specimens.

Nomenclatural notes. Wallis (1933) had doubts about the validity of his species, *I. denikei*, but decided that color characters were constant enough to justify separating the western Ontario specimens from other specimens of *I. confusus*. I recognize the paler color of specimens of *I. denikei* but because the color characters are not supported by any other differences, I regard *I. denikei* as a junior synonym of *I. confusus*.

Classification notes. *Ilybius confusus* is the sister species of *I. incarinatus* which it closely resembles in almost all characters including form of the male genitalia. These species are in turn similar to *I. biguttulus* and I include them together in the same group (see discussion under *I. biguttulus*).

Ecology. Wallis (1933:272) has given the only description of the habitat. The type series of *I. denikei* was taken from along the shore of Long Pine Lake near Ingolf, Ontario. The beetles occurred among plant debris in shallow water along a sandy lake shore near where a small stream entered the lake from a swamp. I have seen a record for flight on 7 July.

Distribution. The range extends along the Atlantic coast from Nova Scotia to Washington, D.C., and westward to the edge of the Great Plains (Map 6). A single specimen from central Nebraska is unexpected but there is no reason to doubt the record.

Ilybius oblitus Sharp, 1882

Ilybius oblitus Sharp 1882:560. Lectotype—here designated, male in BMNH, labelled as follows: specimen pinned to a card labelled “♂ Am. bor. 856”/red rimmed disc “type”/“Sharp Coll. 1905-313”/“Type 856 oblitus Am. bor.”

Selected references. Leng 1920:80; Fall 1927:283; Wallis 1939:197; Young 1954:102.

Description. This species is of moderate size (length 8.9 to 10.7 mm) and relatively

Table 7. Measurements and ratios for selected population samples of *Ilybius oblitus* Sharp.

Locality	N	Length L	Maximum width W	L/W	WC/WS
Massachusetts, New York, New Jersey	12	9.70 (0.28) 9.18–10.06	5.24 (0.14) 4.96–5.40	1.85 (0.03) 1.78–1.89	5.76 (0.46) 5.17–6.78
Michigan and Ohio	8	9.65 (0.55) 8.95–10.66	5.34 (0.17) 5.11–5.62	1.81 (0.06) 1.74–1.89	5.51 (0.20) 5.25–5.81
Missouri, Winona	20	9.50 (0.29) 9.03–10.06	5.18 (0.17) 4.88–5.48	1.84 (0.04) 1.78–1.91	5.58 (0.31) 5.09–6.32

broadly oval shape ($L/W=1.74$ to 1.91). Measurements and ratios for specimens from three population samples are given in Table 7.

Color of dorsal surface piceous to black medially, head with anterior margin and frontal spots and lateral margins of pronotum and elytra reddish, grading shortly into darker color of disc. Antenna and palpi entirely pale. Ventral surface of body reddish to piceous.

Elytron (Fig. 8) with sculpture coarse, lines deeply impressed and broad, meshes of irregular size but for most part small and rounded but some slightly stretched longitudinally basomedially and, on some specimens, meshes just posterad of middle slightly transverse. Meshes with evident microreticulation apically but smooth on basal half.

Prosternal process short and broad, medially narrowly rounded and not carinate; metasternal impression in which it is received short, on most specimens not attaining level of hind margin of mesocoxal cavities. Metasternal wing very narrow, $WC/WS=5.09$ to 6.78 .

Metacoxal plate with striae deeply impressed, dense and elongate, and forming more or less continuous subparallel lines across length of plate. Metacoxal lines relatively little diverging, not reaching metasternum.

Metafemur with short oblique striae on ventral face. Metatibia with ventral face finely and sparsely punctate except for coarse punctures at base and along inner margin: longer metatibial spur subequal to or longer than metatarsomere 1: metatarsomere 1 lacking ventrolateral coarse setae.

MALE: Protarsal claws (Fig. 38) sinuate ventrally, posterior claw with a deep ventrobasal emargination. Metacoxae with median line bearing a small longitudinal keel on posterior portion. Metatarsomeres lacking a dorsolateral bead. Dorsal metatarsal claw (Fig. 52) narrowed more or less evenly to arcuate apex. Sternum 6 (Fig. 20) broadly rounded apically, with a complete marginal bead: surface smooth, lacking rugae or with only faint, broad longitudinal impressions posteriolaterally; posterio-medial keel absent but a light low posterio-medial longitudinal swelling or tumid area evident. Subgenital plate broad apically, it and lateral plates strongly strigate. Genitalia (Fig. 66) with paramere with sucker hairs sparse, of unequal lengths: aedeagus simple, with apex obliquely rounded.

FEMALE: Metatibia along internal margin and metatarsomeres along external margin lacking natatorial setae. Sternum 6 with apical emargination narrow and shallow, sternum margined laterally and on angles of emargination: emargination with lateral angles obtuse, sides slightly compressed in posterior aspect and middle produced into a well developed ridge.



Map 7. Collection localities for *Ilybius oblitus*. Triangle represents a state record.

Variation. No pattern of geographical variation has been observed.

Classification notes. *Ilybius oblitus* shares many characters with *I. biguttulus* but does have some unique features, namely: narrow metasternal wings, short prosternal process, coarse elytral sculpture and an obliquely rounded apex of the aedeagus. Thus, the species is somewhat separated from the other four members of the *I. biguttulus* group. Although male sternum 6 lacks a distinct posteriomedial carina, a faint longitudinal convexity can be discerned on most specimens suggesting either the beginnings of the development of a carina, or the final stages of its loss.

Ecology. I collected several specimens from among emergent grasses and rushes at the edge of a flooded borrow pit in southern New Jersey. The water was clear and warm and the bottom composed of sand covered with plant debris. The only flight record is for a specimen collected at light on 23 June 1907, in Washington, D.C.

Distribution. The range extends from New York to Virginia and west to Kansas (Map 7). Young (1954) gave a single Florida record but doubted its validity.

Ilybius angustior (Gyllenhal, 1808)

Dytiscus angustior Gyllenhal 1808:500. Types in Gyllenhal Collection, Dept. of Entomology, University of Uppsala; types revised and male lectotype designated by Persson 1985. Type area: Sweden.

Ilybius picipes: auctorum, not Kirby, 1837.

Selected references. Larson, 1975; Persson, 1985.

Description. This is a small to moderate sized species (length—7.5 to 10.2 mm) of somewhat elongate shape (L/W—1.81 to 2.03). Measurements on selected population samples are presented in Table 8.

Head black dorsally except frontal spots between eyes and anterior margin reddish: antenna yellow with outer flagellomeres infusate apically (palest specimens with at least apical flagellomere infusate medially); palpi yellow with apical palpomere of each palpus infusate medially on most specimens. Pronotum with disc black, lateral margin narrowly reddish or piceous and evenly darkened onto disc. Elytra of most specimens piceous and not fully black, lateral margins and epipleura reddish: disc may be shiny with a faint metallic sheen or dull. Ventral surface of body piceous to black, legs dark red.

Elytron (Fig. 9) with meshes of sculpture small, laterally rounded but irregular in size and shape; without regular pattern of orientation or stretching and with little tendency of fusion of adjacent meshes. Meshes microreticulate with reticulation shallow and somewhat effaced basally.

Prosternal process of only moderate length, apex acuminate: lateral bead well developed but not especially inflated between procoxae, distinct along lateral margin to apex: process strongly tectiform and sides not noticeably explanate immediately posteriad to procoxae; in ventral aspect shape lanceolate. Metasternum with anteriomedial impression extended posteriorly to level of hind margin of mesocoxal cavities. Metasternal wings broad, WC/WS—2.04 to 2.82 (Table 8).

Metacoxal plate finely reticulate: striae fine and numerous, irregular with considerable joining and intersection of lines: punctures numerous and situated in striae. Metacoxal lines faintly sinuate, elongate but not reaching metasternum.

Metafemur relatively densely punctate but punctures not elongate or linear. Meta-

Table 8. Measurements and ratios for selected population samples of *Ilybius angustior* Gyll.

Locality	N	Length L	Maximum width W	L/W	WC/WS
Alaska, Nome	18	8.36 (0.24) 7.99–8.88	4.37 (0.15) 4.07–4.66	1.92 (0.04) 1.85–2.01	2.35 (0.13) 2.04–2.61
Y.T., Ogilvie Mts.	16	8.74 (0.19) 8.44–9.18	4.47 (0.08) 4.29–4.59	1.95 (0.04) 1.89–2.03	2.46 (0.12) 2.27–2.69
N.W.T., Reindeer Sta.	40	8.26 (0.29) 7.55–8.88	4.35 (0.14) 4.00–4.81	1.90 (0.04) 1.82–1.97	2.28 (0.11) 2.05–2.66
N.W.T., Aklavik	52	8.45 (0.26) 7.99–9.10	4.36 (0.16) 4.00–4.88	1.94 (0.05) 1.82–2.02	2.27 (0.11) 2.08–2.58
N.W.T., Richards I.	15	8.37 (0.24) 7.77–8.80	4.40 (0.13) 4.07–4.59	1.90 (0.03) 1.84–1.97	2.33 (0.10) 2.20–2.50
N.W.T., Eskimo Pt.	19	8.61 (0.23) 8.21–9.03	4.48 (0.13) 4.29–4.74	1.92 (0.04) 1.82–1.97	2.37 (0.07) 2.26–2.47
N.W.T., Coppermine	44	8.20 (0.22) 7.77–8.58	4.23 (0.11) 4.00–4.44	1.94 (0.03) 1.89–2.04	2.38 (0.13) 2.16–2.68
N.W.T., Ft. Smith	20	8.79 (0.26) 8.44–9.47	4.68 (0.17) 4.29–5.03	1.88 (0.04) 1.81–1.97	2.50 (0.14) 2.27–2.82
Alberta, Manning	20	8.96 (0.30) 8.40–9.44	4.75 (0.17) 4.44–5.04	1.89 (0.03) 1.82–1.93	2.24 (0.11)* 2.10–2.47
Manitoba, Churchill	19	8.66 (0.32) 7.99–9.18	4.52 (0.19) 4.14–4.88	1.92 (0.04) 1.86–2.00	2.48 (0.10) 2.25–2.61
Quebec, Gt Whale R.	16	8.92 (0.29) 8.36–9.47	4.68 (0.13) 4.44–4.88	1.91 (0.03) 1.85–1.97	2.53 (0.10) 2.38–2.73
Quebec, Harrington Hr.	20	8.95 (0.28) 8.44–9.55	4.67 (0.12) 4.44–4.88	1.92 (0.03) 1.85–1.97	2.52 (0.10) 2.30–2.78
Newfoundland, N. Penn. (♂)	20	9.42 (0.29) 8.88–9.84	4.88 (0.16) 4.59–5.11	1.93 (0.03) 1.88–2.00	2.47 (0.10) 2.25–2.61
Newfoundland, Avalon Penn.	20	9.37 (0.39) 8.73–10.21	4.91 (0.18) 4.59–5.33	1.91 (0.04) 1.84–1.97	2.49 (0.13) 2.21–2.72

* From Larson (1975), WS includes width of coxal rim.

tibia with a series of coarse punctures extending entire length of ventral face, density of punctures various but on average specimens of *I. angustior* have the metatibia more densely and coarsely punctate than do specimens of *I. picipes*. Longer metatibial spur subequal to or slightly shorter than metatarsomere 1. Metatarsomere 1 without dorsomedial setae but with from 1 to several stout spines along ventrolateral margin.

MALE: Protarsus (Fig. 39) with posterior claw narrower and more arcuate than anterior, both straighter than respective claws of *I. picipes*. Metacoxae with a small posteriomedial keel. Metatarsomeres with a dorsolateral bead or ridge. Metatarsal claws (Fig. 53) with dorsal claw blade-like, shallowly emarginate externobasally and evidently broadened medially. Sternum 6 (Fig. 21) with a posteriomedial longitudinal keel, hind surface lateral to keel with strong longitudinal rugae. Subgenital plate broad and truncate apically, broader than that of *I. picipes*, longitudinally strigate laterally; lateral plates longitudinally strigate. Genitalia (Fig. 67) with paramere narrow, with

sucker hairs on mesal face: aedeagus narrow, apex slightly reflexed ventrally and evidently narrowed in lateral aspect.

FEMALE: Metafemur along internal margin and metatarsomeres along outer margin lacking natatorial setae. Sternum 6 (Fig. 28) with posteriomedial emargination well developed, its sides not appreciably pinched in posterior aspect: marginal bead complete around lateral angles of emargination. Gonocoxa with dorsal margin more curved at base and apex more abruptly pointed than that of *I. picipes*.

Variation. The occurrence of two additional very similar species, *I. picipes* (Kirby) and *I. churchillensis* Wallis, compounds the problem of interpreting patterns of variation in this species because supposed intraspecific variation may be due to misidentification. For example, I confused *I. picipes* with *I. angustior* in the past (Larson, 1975) and am certain that some of my identifications of female specimens are still wrong as I cannot separate the two consistently without association with males. Also, species of this complex show some parallel patterns of variation in regions of sympatry.

The smallest specimens of *I. angustior* are from along the western arctic mainland coast. Specimens from more southerly localities are considerably larger, for example mean length of specimens along a north-south transect are: Reindeer Station, N.W.T.—8.26 mm; Ft. Smith, N.W.T.—8.79 mm; Manning, Alta.—8.96 mm. Specimens of *I. churchillensis* also increase in size from north to south (Reindeer Station, N.W.T.—7.78 mm; Churchill, Man.—8.01 mm). Over the boreal region, the mean size of *I. angustior* specimens is fairly uniform at about 8.8 to 9.0 mm but specimens from the island of Newfoundland are noticeably larger (mean about 9.4 mm). *I. picipes*, which is largely sympatric with *I. angustior* over the boreal region, shows a similar but less pronounced tendency towards larger size on the island of Newfoundland; however, this is influenced by the omission of female specimens from Newfoundland as their identity is uncertain.

The ratio WC/WS varies only slightly, tending to be smaller in the low arctic than in boreal portions of the range, but the differences in population means are slight.

Similarity in the pattern of variation in length and WC/WS between populations of *I. angustior* and *I. churchillensis* can be seen in Figure 74. In spite of the variation, in localities of sympatry the two species can be separated fairly reliably on the basis of these measurements.

Fortunately, the diagnostic characters for the separation of male *I. angustior* from males of *I. picipes*, medially dilated dorsal metatarsal claw, and narrow reflexed apex of aedeagus, while slight, are remarkably constant over the wide holarctic range.

Nomenclatural notes. Old World synonymy is given by Zimmermann (1920) and is not repeated here. *I. picipes* (Kirby) is not a synonym of *I. angustior* and many holarctic records of *I. angustior* are probably based on misidentified specimens of *I. picipes*, some of my previous records certainly are (Larson, 1975; Larson and Colbo, 1983).

Classification notes. Persson (1985) has shown that most previous authors have defined *I. angustior* too broadly and that over much of the Holarctic distribution two sympatric sibling species occur (see discussion under *I. picipes* (Kirby)). In addition, in the arctic mainland of North America, west of Hudson Bay, *I. angustior* co-occurs with or is replaced by another very similar species, *I. churchillensis* Wallis.

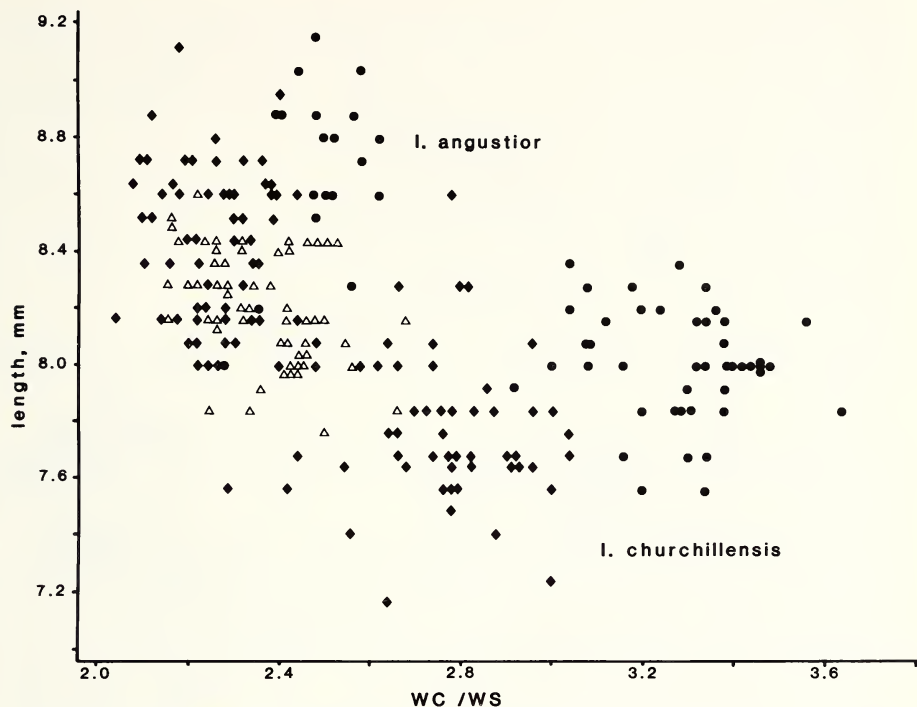
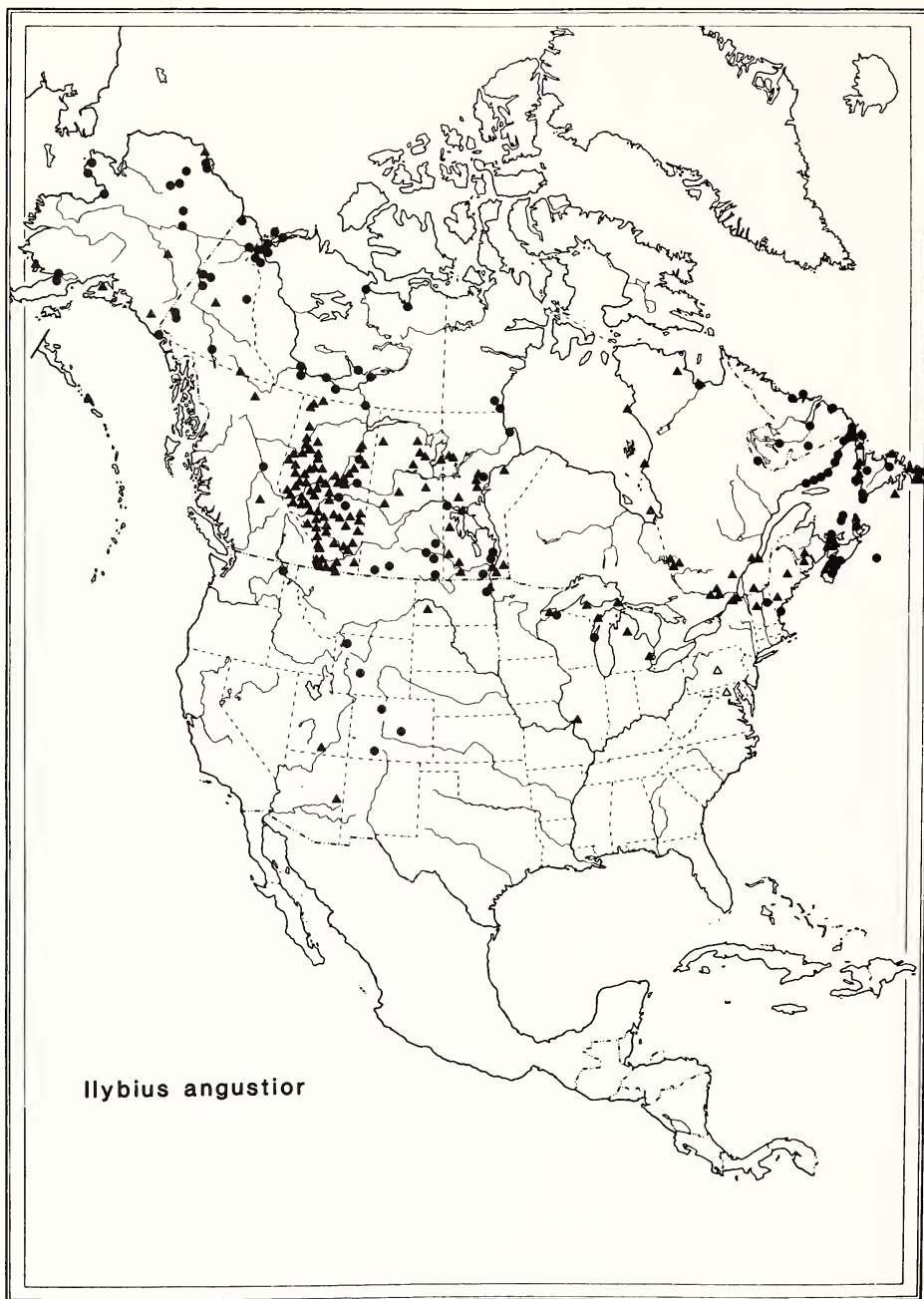


Fig. 74. Scatter diagram of length versus width for specimens of *I. angustior* and *I. churchillensis* from selected localities: closed circle—Churchill, Manitoba (both species); closed diamonds—Mackenzie Delta, N.W.T. (both species); open triangles—Coppermine, N.W.T. (*I. angustior* only).

The aggregate range of these species, which comprise the *I. angustior* group in North America, extends from the low arctic to the southern boreal region with *I. churchillensis* in the low arctic being the most northerly, *I. angustior* from the southern limits of the low arctic into the mid-boreal and northern prairie regions and along the Rocky Mountains, and *I. picipes* in mid- to southern boreal areas and maritime areas.

Ecology. This species occurs primarily in forested regions, in lentic sites where the water is shaded by dense stands of emergent vegetation, usually *Carex*. Specimens have been collected from prairie ponds but are seldom common in such habitats and are usually in transitional areas such as parkland or fescue prairie. The range of habitat overlap with other *Ilybius* species given by Larson (1985) is too broad and most co-occurrences with *I. discedens* are probably referable to *I. picipes*. Nilsson (1981) has described the larva and the life history in Sweden. Flight records extend from June 28 to July 14, with one record for October 1.

Distribution. The range is holarctic and primarily boreal. In North America the distribution extends from Newfoundland and Sable Island to Nome, Alaska, and from the arctic coast in the west, south along the Rocky Mountains to Colorado and New Mexico (Map 8).



Map 8. North American collection localities for *Ilybius angustior*. Closed circles—record confirmed by examination of male genitalia and metatarsal claws; closed triangles—record based on female specimens or not confirmed by examination of male genitalia and metatarsal claws, some of these records may be based on misidentified *I. picipes*; open triangle—state record.

Table 9. Measurements and ratios for selected population samples of *Ilybius churchillensis* Wallis.

Locality	N	Length L	Maximum width W	L/W	WC/WS
N.W.T., Reindeer Sta.	48	7.78 (0.27)	3.96 (0.13)	1.96 (0.04)	2.79 (0.13)
		7.18–8.58	3.70–4.29	1.89–2.07	2.44–3.04
Manitoba, Churchill	40	8.01 (0.20)	4.04 (0.11)	1.98 (0.03)	3.30 (0.10)
		7.55–8.36	3.85–4.29	1.90–2.08	3.00–3.64

Ilybius churchillensis Wallis, 1939

Ilybius churchillensis Wallis 1939:195. (Holotype—male, Churchill, Manitoba, in CNC.) (Type examined.)

Selected references. Wallis 1939:195.

Description. This species is similar to *I. angustior* but specimens are smaller (L—7.2 to 8.6 mm), narrower (L/W—1.89 to 2.08) and have narrower metasternal wings (Table 9, Fig. 74).

Color of dorsal surface mainly black, relatively shiny, specimens from the type locality with a green reflection but all other specimens examined lack green sheen. Frontal spots, anterior margin of clypeus, mouthparts and lateral margin of pronotum rufescent; elytron with lateral margin faintly piceous. Antenna yellow with distal antennomeres (on most specimens beginning antennomeres 3–5) distinctly infusate; palpi of most specimens with distal palpomere infusate apically. Legs dark rufous to piceous.

Elytron with meshes of sculpture coarser and more irregular in shape than on *I. angustior*, meshes without evident pattern of orientation or stretching; microreticulation evident apically but surface relatively shiny basally where microreticulation is only faintly impressed or absent.

Prosternal process short, apex acuminate and somewhat deflected upwards behind procoxae and out of plane of midline of prosternum in lateral aspect. Metasternal impression not or only just attaining level of hind margin of mesocoxal cavities. Metasternal wing narrower than in *I. angustior*, WC/WS—2.44 to 3.64.

Metacoxal plates with striae sparser and shorter than in *I. angustior*; striae irregularly oriented and variously interconnected especially medially on plate; on some specimens striae obscured by coarse reticulation and transverse rugae of plate; small punctures present both between and in striae. Metacoxal lines slightly arcuate anteriorly, finely traceable to metasternum or not.

Metafemur finely punctate, without striae. Metatibia with a series of coarse punctures along length of ventral face, punctures either forming a narrow medial series or punctate area expanded over most of ventral surface. Metatibial spurs slightly shorter than metatarsomere 1. Metatarsomere 1 with one to several ventrolateral setae.

MALE: Protarsal claws (Fig. 40) slender, similar to those of *I. angustior*. Metacoxae with a small medial keel on posterior portion of medial line. Metatarsomeres with a dorsolateral ridge: metatarsal claws (Fig. 54) slender, dorsal claw narrow and blade-like, its ventral (outer) margin not or only slightly expanded medially. Sternum 6 with a posteriomedial keel, hind margin laterad to keel with coarse longitudinal

rugae. Subgenital plates strigate. Aedeagus (Fig. 68) slender, apex slightly reflexed ventrad and narrowly rounded.

FEMALE: Metatibia along inner margin and metatarsomeres externally lacking natatorial setae. Sternum 6 with medial emargination well developed, lateral angles rounded with a complete marginal bead: sides of emargination slightly pinched in posterior aspect.

Variation. This species shows considerable variation between the few population samples which I have examined. Measurements and ratios for the larger population samples examined are given in Table 9. Specimens from Churchill, Manitoba, have a distinct green reflection and are relatively large with narrow metasternal wings. Specimens from all other localities are entirely black without a green sheen. Towards the northwest, specimens are smaller but have relatively broader metasternal wings and tend to converge on *I. angustior* specimens which are also very small in this area (Fig. 74).

Nomenclatural notes. The species was described from 3 specimens (CNC) which I have examined. There is a long series of specimens from Churchill (O. Bryant, collector) in CAS, some of which I have, with permission of Dr. D. Kavanaugh, deposited in CNC, MUN, and USNM.

Classification notes. Male characters such as shape of dorsal metatarsal claw and apex of aedeagus are almost identical between *I. angustior* and *I. churchillensis* suggesting that *I. churchillensis* is closer to *I. angustior* than to *I. picipes*.

Ilybius churchillensis appears to replace *I. angustior* in the low arctic region west of Hudson Bay. Both species have been collected from several localities situated at the boundary between the low arctic and boreal regions. Although habitat data does not exist with most specimens, the fact that specimens of the two species have been collected on different dates or slightly different localities even when found in a region of sympatry, suggests that there is some habitat segregation or differentiation between the two species supporting the morphological segregation.

Ecology. The habitat has not been described. At Reindeer Station, N.W.T., A. Smetana (pers. comm.) collected specimens of *I. churchillensis* in tundra pools in upland habitat while collections in the Mackenzie River valley contained only *I. angustior*. There are no flight records.

Distribution. The species is known from only a few localities on the western arctic mainland, ranging from Churchill, Manitoba, to northern Alaska (Map 5).

Ilybius picipes (Kirby, 1837)

Colymbetes picipes Kirby 1837:17. Lectotype: selected by Persson 1985; male in BMNH from H.T. (Hudson Bay Territories), North America. (Type examined.)

Selected references. Persson 1985:266.

Description. This species is very similar to *I. angustior* and only the males can be recognized with confidence: the females are almost indistinguishable. Length 8.0 to 9.5, L/W—1.84 to 2.01. Measurements on selected population samples are given in Table 10.

Color averaging darker than on *I. angustior*, specimens usually with dorsal surface black medially, never with a metallic sheen. Antenna yellow with at least apical

Table 10. Measurements and ratios for selected population samples of *Ilybius picipes* Kirby.

Locality	N	Length L	Maximum width W	L/W	WC/WS
Alaska, King Salmon	20	8.75 (0.25)	—	—	2.55 (0.08)
		8.36–9.18			2.40–2.67
Southern Ontario	13	8.89 (0.30)	4.70 (0.18)	1.89 (0.03)	2.62 (0.11)
		8.29–9.32	4.37–5.03	1.84–1.94	2.40–2.78
Michigan	9	8.91 (0.25)	—	—	2.56 (0.14)
		8.58–9.47			2.37–2.81
Labrador (males)	11	8.73 (0.36)	4.55 (0.20)	1.92 (0.02)	2.62 (0.09)
		8.29–9.32	4.29–4.88	1.89–1.97	2.42–2.74
Newfoundland (males)	20	9.05 (0.32)	4.72 (0.20)	1.92 (0.04)	2.62 (0.10)
		7.99–9.47	4.14–5.03	1.86–2.01	2.50–2.86

flagellomere infusate medially: palpi entirely pale or with apical palpomere of each palpus infusate. Ventral surface of body piceous to black: legs dark rufous to piceous.

Elytron (Fig. 10) with meshes of sculpture small, irregular in size and shape but generally somewhat rounded: lines deeper than in *I. angustior* and meshes more convex: microreticulation present apically but obsolete basally on most specimens. Elytra less shiny macroscopically, on average, than those of *I. angustior*.

Prosternal process and metasternum similar to that of *I. angustior* but differing as follows: lateral bead slightly broader between and behind procoxae, in ventral aspect process broader with sides evidently explanate at point of maximum width and shape of process more cordate. Metasternal wing broad, WC/WS—2.37 to 2.81, population means greater than for *I. angustior* (Table 10).

Metacoxal plate with striae elongate, irregular and variously intersecting to form an irregular meshwork. Metacoxal lines slightly sinuate, not or only faintly traceable to metasternum.

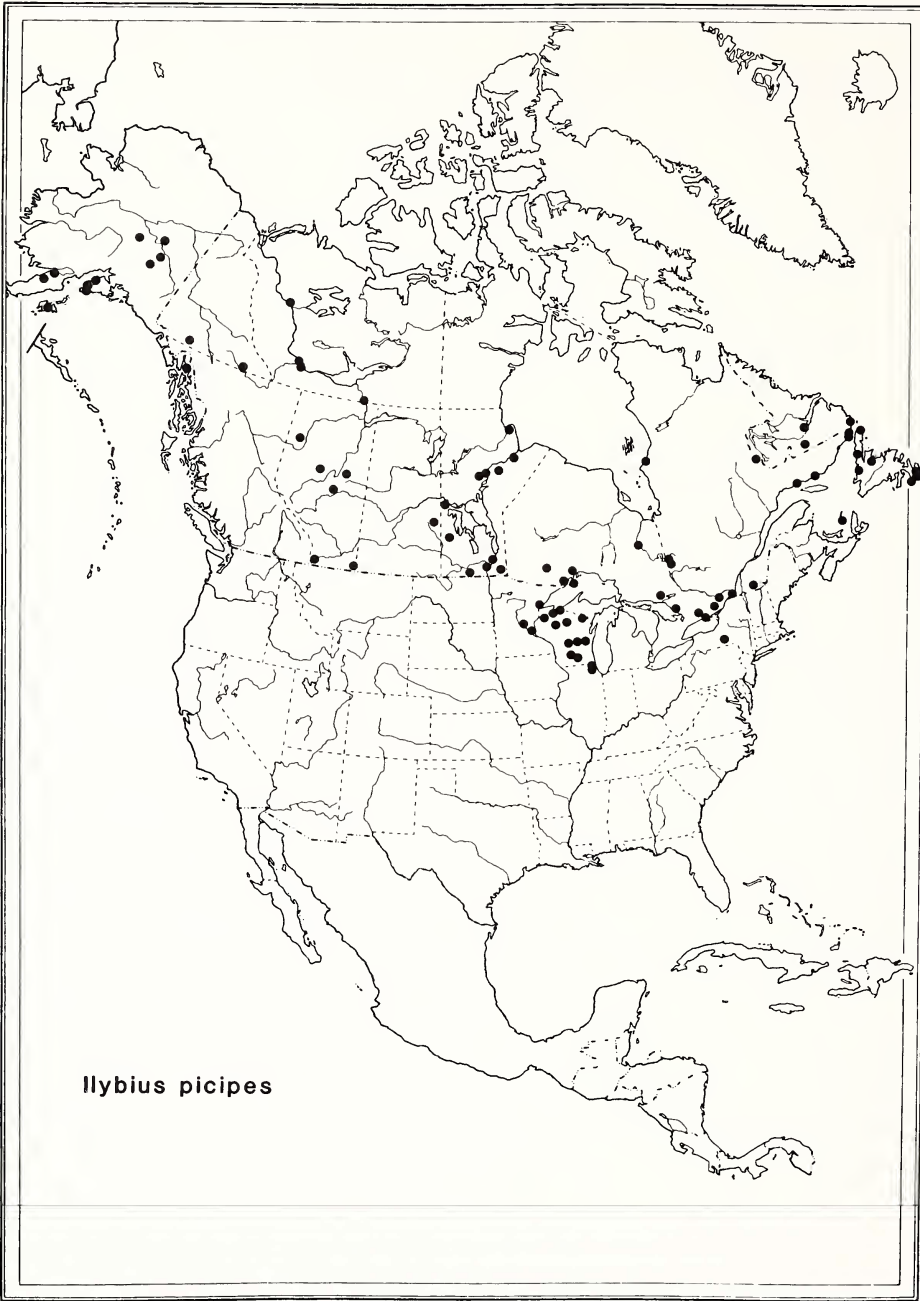
Metafemur punctate but lacking short, oblique striae. Metatibia with coarse punctures along entire ventral face. Larger metatibial spur subequal to metatarsomere 1. Metatarsomere 1 with one to several spines along ventroexternal margin.

MALE: Protarsal claws (Fig. 42) shorter, broader and more arcuate than those of *I. angustior*. Metacoxae with a small posteriomedial longitudinal keel. Metatarsomeres with a dorsoexternal ridge, ridge narrower than on *I. angustior*, especially on metatarsomere 4. Dorsal metatarsal claw (Fig. 55) narrower than in *I. angustior*, not evidently widened near middle. Sternum 6 and paramere as in *I. angustior*. Subgenital plate narrower apically than in *I. angustior*. Aedeagus (Fig. 69) with apex subparallel, bluntly pointed and not reflexed ventrally in lateral aspect.

FEMALE: Similar to *I. angustior*. Gonocoxa with dorsal margin straighter and apex more evenly tapered to a point than in *I. angustior*.

Variation. This is discussed under *I. angustior*.

Nomenclatural notes. *Ilybius picipes* has long been considered a synonym of *I. angustior*, but Persson (1985) has shown that the name refers to a valid species. I examined the type specimens without recognizing the validity of the species (Larson, 1975).



Map 9. North American collection localities for *Ilybius picipes*. Note—some of the closed triangles of Map 9 may represent collection records of misidentified specimens of *I. picipes*.

Table 11. Measurements and ratios for selected population samples of *Ilybius quadrimaculatus* Aubé.

Locality	N	Length L	Maximum width W	L/W	WC/WS
SW Alberta, & SE B.C.	10	10.70 (0.22)	5.67 (0.18)	1.89 (0.03)	2.55 (0.07)
		10.24–11.04	5.36–6.00	1.84–1.93	2.48–2.68
B.C., Mission City	14	10.07 (0.34)	5.41 (0.17)	1.86 (0.03)	2.71 (0.13)
		9.47–10.66	5.03–5.70	1.81–1.91	2.48–2.95
Alaska, Unalaska	15	10.38 (0.25)	5.50 (0.16)	1.89 (0.04)	2.73 (0.07)
		9.99–10.80	5.25–5.77	1.82–1.97	2.62–2.84

Classification notes. Initially on learning of Persson's conclusion that *I. picipes* was a good species, I had difficulty accepting its validity. However, after examining many hundreds of specimens from across North America, I found the slight differences in shape of the male pro- and metatarsal claws and aedeagus to be consistent, even in localities where both forms occur in sympatry. The distributions of the two differ slightly, with *I. picipes* tending to be more southerly or maritime in distribution than *I. angustior*, although *I. angustior* is the only species occurring in the Rocky Mountains of the contiguous United States.

Ecology. *Ilybius picipes* occurs in peatland pools in Newfoundland and Labrador while *I. angustior* has a broader range of habitats which include both peatland pools and marshes. Ecological distinctions between the two species have not been made elsewhere because of the difficulty involved in recognizing the species in the field. I have seen flight records for 4 and 27 June.

Distribution. *Ilybius picipes* has a holarctic distribution. In North America it is transcontinental in the boreal region. Collection records are indicated in Map 9. Only those collections that contain male specimens are indicated.

Ilybius quadrimaculatus Aubé, 1838

Ilybius quadrimaculatus Aubé 1838:274. (Type area: "Amerique septentrionale".)
Type not located.

Selected references. Larson 1975:376.

Description. This is a moderate sized (L—9.5 to 11.1 mm), elongate-oval (L/W—1.81 to 1.97) species. Ratios and measurements for three population samples are given in Table 11.

Color of body very dark, mainly black with anterior margin of clypeus, labrum, frontal spots, narrow lateral margin of pronotum and legs, dark rufous. Elytron with small postmedial vitta and subapical crescentic spot distinct on most specimens: disc medially faintly cupreous or aeneous on some specimens. Antenna rufous except antennomeres 5 to 11 infusate apically (palest specimens with at least antennomeres 10 and 11 infusate apically). Palpi pale with terminal palpomeres infusate apically.

Elytron (Fig. 11) shiny, meshes of sculpture relatively small, irregular in size and shape, on basal half of disc some meshes elongated or oblique but without forming distinct pattern of longitudinal stretching.

Prosternal process elongate and apically acuminate; in cross section strongly tectiform but narrowly rounded medially; sparsely setose basally but glabrous apically. Metasternal impression well developed and posteriorly attaining level of hind margin of mesocoxal cavities. Metasternal wings moderately broad (WC/WS—2.48 to 2.95).

Metacoxal plate shiny, with lightly impressed isodiametric sculpture and distinct but short and mainly separated striae, striae fine and relatively sparse; punctation evident. Metacoxal lines slightly arcuate anteriorly, not attaining metasternum.

Metafemur with numerous distinct but small punctures, striae absent. Metatibia with coarse punctures on basal third to half of ventral face, distally with sparse fine punctures except for row of coarse punctures along ventral mesal margin. Longer metatibial spur slightly longer than metatarsomere 1. Metatarsomere 1 without coarse ventral setae along ventrolateral margin.

MALE: Protarsal claws as in Figure 41: anterior claw with a distinct ventrobasal sinus; posterior claw shorter and narrower than anterior, with a distinct ventrobasal emargination. Metacoxae with a small posteriomedial longitudinal keel. Metatarsomeres 1 to 4 with a dorso-external bead: dorsal metatarsal claw (Fig. 56) evenly narrowed to curved apex. Sternum 6 (Fig. 23) with a large posteriomedial longitudinal keel, hind margin lateral to keel with coarse longitudinal rugae: marginal bead obsolete medially. Subgenital plate relatively narrow, truncate to shallowly and broadly emarginate apically, it and lateral plates strongly longitudinally rugose. Genitalia (Fig. 70) with paramere bearing short adhesive setae on mesal face: aedeagus elongate, longer than paramere and with apex spear-shaped in dorsal aspect.

FEMALE: Metatibia with mesal margin and metatarsomeres 1 to 3 with outer margins lacking natatorial setae. Sternum 6 (Fig. 29) shallowly and narrowly emarginate apically, lateral angle of emargination bluntly rounded and obtuse: in posterior aspect sides of emargination slightly pinched and medial portion raised as a distinct knob, this elevated knob extended anterad on sternum as a low but evident convexity traceable on many specimens over most of midline of sternum, many specimens with a fine longitudinal impression along middle of convexity just anterad of medial knob: lateral bead continuous around lateral angles of emargination.

Variation. The largest specimens are from western Alberta and southeastern British Columbia. These specimens also have slightly broader metasternal wings than those from more westerly localities. Too few population samples are available from central British Columbia to determine if variation in these characters is gradational or abrupt. The distinctive male genitalia is constant throughout the range supporting conspecificity.

Nomenclatural notes. I did not locate the type specimen. Neither the original description (Aubé, 1838) or the redescrptions by Crotch (1873) and Sharp (1882) provide sufficient detail to tie the name to the current species. Fall (1927) is the first to provide an adequate diagnosis for recognition of the species but he did not indicate on what basis he determined the application of the name. The current usage should be considered provisional until the type is examined.

Classification notes. This species shares with members of the *I. angustior* complex infusate antennae and palpi and a similar form of male sternum 6. On the other hand, the spear-like apex to the aedeagus in *I. quadrimaculatus* is distinctive and the metatibial punctation is reduced beyond that seen in any other North American member of the complex.

Table 12. Measurements and ratios for selected population samples of *Ilybius pleuriticus* LeConte.

Locality	N	Length L	Maximum width W	L/W	WC/WS
Newfoundland, pooled	20	11.40 (0.41)	6.01 (0.24)	1.90 (0.04)	2.84 (0.14)
		10.65–11.91	5.55–6.44	1.81–1.97	2.56–3.15
Labrador, pooled	20	11.34 (0.50)	6.00 (0.24)	1.89 (0.05)	2.75 (0.10)
		10.21–11.99	5.48–6.36	1.76–1.97	2.56–2.95
N.B., Fred’cton	17	11.52 (0.43)	6.12 (0.26)	1.88 (0.04)	2.70 (0.03)
		10.58–12.28	5.48–6.44	1.81–2.00	2.42–2.95
Alberta, Smith	20	11.75 (0.47)	6.27 (0.28)	1.88 (0.04)	2.53 (0.10)*
		10.72–12.56	5.76–6.96	1.81–1.95	2.39–2.73

* From Larson (1975), WS includes width of coxal rim.

The range of *I. quadrimaculatus* suggests the possibility of occurrence in the eastern Palaearctic region. However, I have not seen Old World specimens nor have I seen any Palaearctic species that approaches *I. quadrimaculatus* in aedeagal shape.

Ecology. This species occurs among emergent vegetation of permanent marshes, beaver ponds and backwater depositional zones of very slowly flowing streams. Specimens are often found in sites where the water is cool and there is some degree of flushing either by springs or the proximity of larger streams. There are no records of flight.

Distribution. The range of this species extends from the Aleutian Islands south to central California and east to the eastern slopes of the Rocky Mountains (Map 6).

Ilybius pleuriticus LeConte, 1850

Ilybius pleuriticus LeConte 1850:213. Holotype—female in MCZ labelled: pale blue disc/“♀” /“Type 6070”/“var. pleuriticus LeC.” (Type examined.) Type locality—Lake Superior.

Ilybius inversus Sharp 1882:552. Holotype—male, Hudson Bay, in BMNH (Type examined.)

Selected references. Larson 1975:375.

Description. Size large (L—10.2 to 12.6 mm), body moderately broad (L/W—1.76 to 2.00). Measurements for selected population samples are given in Table 12.

Color of dorsal surface piceous medially, with a faint brassy sheen on some specimens; lateral margins of body evidently reddish. Head with frontal spots, anterior portion of clypeus and labrum, rufous. Antenna and palpi pale, without infuscation. Pronotum with lateral margins broadly reddish, most specimens with anteriolateral angle red. Elytron with epipleuron and lateral margin broadly reddish, on some specimens reddish area extends onto disc almost to level of sublateral vitta: lateral and subapical spots evident. Ventral surface variously reddish to piceous: legs reddish.

Elytron with sculpture various, some specimens with meshes small and irregular in size but similar over most of disc; most specimens with meshes basally and medially very irregular in size and shape and appearing as though fusion of adjacent meshes has occurred to produce fewer elongated or curved meshes (Fig. 12); secondary reticulation present but on many specimens is more or less effaced on basal portions of elytron.

Prosternum with process moderately elongate and apically acuminate, tectiform in cross section with medial convexity narrowly rounded; lateral bead of process slightly broadened between and behind procoxae. Metasternal impression extending posteriorly to level of hind margin of mesocoxal cavities. Metasternal wings broad, WC/WS—2.5 to 3.2.

Metacoxal plates with short to moderately elongate, dense but mainly separate striae: sparse punctation evident. Metacoxal lines not attaining metasternum but longer than in *I. subaeneus*.

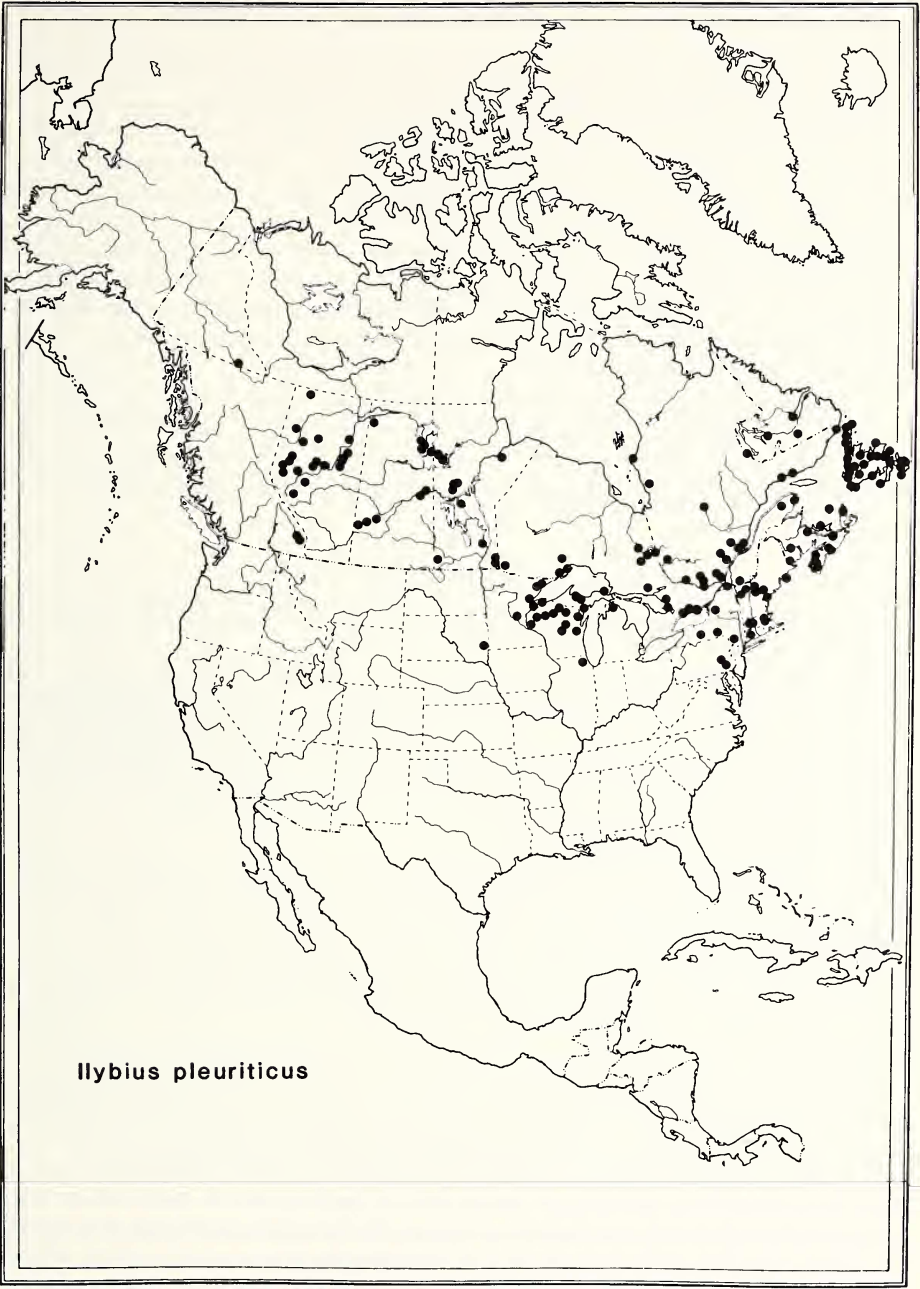
Metafemur finely punctate, a few punctures along hind margin obliquely elongated forming fine striae. Metatibia with punctures extending length of ventral face on most specimens but punctures irregular in size, usually coarse basally becoming finer towards distal half, or on some specimens punctures may be more or less obsolete on distal half. Longer metatibial spur slightly longer than metatarsomere 1. Metatarsomere 1 lacking ventrolateral coarse setae.

MALE: Protarsal claws as in Figure 43: anterior claw with basoventral sinus small; posterior claw with a distinct basoventral emargination. Metacoxae with a small medial keel. Metatarsomeres 1 to 4 with a dorsoventral ridge: dorsal metatarsal claw (Fig. 57) blade-like, slightly sinuate ventrally. Sternum 6 (Fig. 24) with a short posteromedial longitudinal carina: posteriolateral portions without longitudinal rugae or with a few shallow rugae but punctures evident: apex broadly rounded or subtruncate medially; marginal bead fine or obsolete medially. Subgenital plate truncate or shallowly emarginate apically, it and lateral plates with strong longitudinal rugae. Genitalia (Fig. 71) with paramere bearing numerous large, adhesive suckers along ventral margin: aedeagus short and blunt.

FEMALE: Metatibia with internal margin and metatarsomeres with external margins lacking natatorial setae. Sternum 6 (Fig. 30) relatively deeply emarginate medially; sides of emargination distinctly pinched in posterior aspect with middle somewhat produced: marginal bead of sternum broken or obsolete on externoapical angles of emargination and not traceable on most individuals. (On some specimens bead is shallow but evident on outer angles of medial emargination.)

Variation. This large species does not show any significant pattern of geographical variation over its range. One character with some individual variation is the lateral beading of sternum 6 of the female. The majority have the bead obsolete or broken just laterad of the outer angle of the medial emargination which provides a good character for identification. The bead is complete but shallow on some specimens, most frequently occurring on specimens from northern Quebec, Labrador and Newfoundland where up to 10% of specimens may have the bead more or less complete.

The extent of punctation of the ventral face of the metatibia also varies individually. The medial punctures are smaller distally on most specimens but are large enough throughout that a distinct series of punctures can be recognized along the entire length of the ventral surface. However, on a few specimens, the punctures are very small distally, almost as small as the micropunctuation of the metatibia of specimens of the *I. biguttulus* group. Such individuals can usually be recognized as *I. pleuriticus* because the punctures gradually become smaller from base to apex so that there is still evidence of a longitudinal series. Also, there are usually a few coarser punctures distally in the series. Such an inequality of distal puncture size does not occur in specimens of the *I. biguttulus* group.



Map 10. Collection records for *Ilybius pleuriticus*.

Classification notes. I associate *I. pleuriticus* with *I. subaeneus* because of similarities in color, sculpture, and certain sexual characters of the males such as the margined metatarsomeres, parameres with sucker hairs and similar forms of aedeagus. These species also share many of these features with the palaearctic *I. ater*.

Ecology. This species occurs in a rather wide range of permanent, lentic habitats, including *Carex* and rush filled marshes, amongst emergent vegetation along sheltered lake shores, and at the edges of larger ponds in peatlands. The association of *I. pleuriticus* and *I. discedens* indicated by Larson (1985) is due to both occurring in peatland ponds. Generally *I. discedens* is in smaller, colder pools and among *Sphagnum* while specimens of *I. pleuriticus* are usually in more sun-warmed sites and among emergent vascular plants so that there is a habitat segregation, although it may be narrow and both species are often taken in the same collection. Flight records exist for 30 May and 7 and 15 July.

Distribution. This species occurs from Newfoundland to the Yukon Territories in the boreal zone (Map 10). There is a specimen in the USNM labelled "Ft. Davis, Phantom L., Davis Mts., June 20, 1916, F. M. Gage." This Texas record is so far removed from any other collection locality that it must certainly be an error.

Ilybius subaeneus Erichson, 1837

Ilybius subaeneus Erichson 1837:156. (Type locality: Berlin, Brandenburg, Germany.) (Type not seen.)

Ilybius viridianeus Crotch 1873:411. (Type locality: not restricted, described from specimens from Kansas and Hudson's Bay. Types not found in ANSP or MCZ.)

Ilybius suffusus Crotch 1873:411. Holotype—female, in ANSP, labelled: "I.T./"IL. suffusus Cr."/ "HOLOTYPE, *Ilybius suffusus* Crotch 1873:411, det. D. Larson 1987." Type area given as "Indian Territory." **NEW SYNONYMY.**

Selected reference. Larson 1975:374.

Description. This is a moderately large (L—9.2 to 11.1 mm), oval (L/W—1.76 to 1.92) species characterized by a greenish reflection of the dorsal surface of the body. Measurements and ratios for selected population samples are given in Table 13.

Body dorsally mainly piceous to black with a distinct greenish sheen on most specimens. Anterior portion of head, frontal spots and lateral margins of pronotum and elytra reddish. Antenna and palpi entirely yellow. Ventral surface piceous. Legs reddish.

Elytron (Fig. 13) with meshes small, irregular in size and shape and without as pronounced a tendency of longitudinal or lateral elongation as seen in *I. pleuriticus*: meshes not longitudinally stretched on basomedial portion of disc.

Prosternal process elongate, acutely pointed apically: medial convexity narrower than in *I. pleuriticus*, carinate on apical half of process: lateral bead not or only slightly inflated between and behind procoxae. Metasternal impression well developed and extending posteriorly to level of hind margin of mesocoxal cavities. Metasternal wings broad, WC/WS—2.32 to 2.65.

Metacoxal plate with short striae, striae longest, densest and somewhat interconnected laterally, shorter and more or less isolated mesad on plate. Metacoxal lines short, disappearing well posterad of metasternum.

Metafemur with small punctures, some punctures along posterior margin elongate

Table 13. Measurements and ratios for selected population samples of *Ilybius subaeneus* Erichson.

Locality	N	Length L	Maximum width W	L/W	WC/WS
Labrador, Minipi L.	20	10.44 (0.22)	5.59 (0.14)	1.87 (0.02)	2.67 (0.15)
		10.06–10.80	5.33–5.77	1.82–1.91	2.45–3.00
Quebec, Mt. Albert	10	9.96 (0.20)	5.41 (0.13)	1.84 (0.04)	2.77 (0.09)
		9.62–10.29	5.11–5.55	1.76–1.90	2.63–2.89
N.W.T., Reindeer Sta.	20	9.83 (0.28)	5.34 (0.14)	1.84 (0.04)	2.56 (0.08)
		9.18–10.36	5.03–5.55	1.76–1.92	2.38–2.69
Saskatchewan, pooled	20	10.16 (0.29)	5.52 (0.17)	1.84 (0.03)	2.52 (0.09)
		9.62–10.16	5.10–5.77	1.78–1.92	2.28–2.69
Alberta, Peace R.	20	10.46 (0.22)	5.62 (0.14)	1.86 (0.03)	2.43 (0.08)*
		9.92–10.96	5.20–5.92	1.82–1.91	2.32–2.65
B.C., Tanzilla R.	4	9.51 (0.64)	5.05 (0.36)	1.88 (0.02)	2.63 (0.12)
		8.88–10.06	4.74–5.40	1.86–1.90	2.54–2.80
Colorado, Longs Peak	21	10.74 (0.23)	5.80 (0.13)	1.85 (0.03)	2.70 (0.10)
		10.29–11.10	5.55–5.99	1.79–1.92	2.52–2.90
Finland	4	9.90 (0.13)	—	—	2.50 (0.11)
		9.77–10.06			2.36–2.63

* From Larson (1975), WS includes coxal rim.

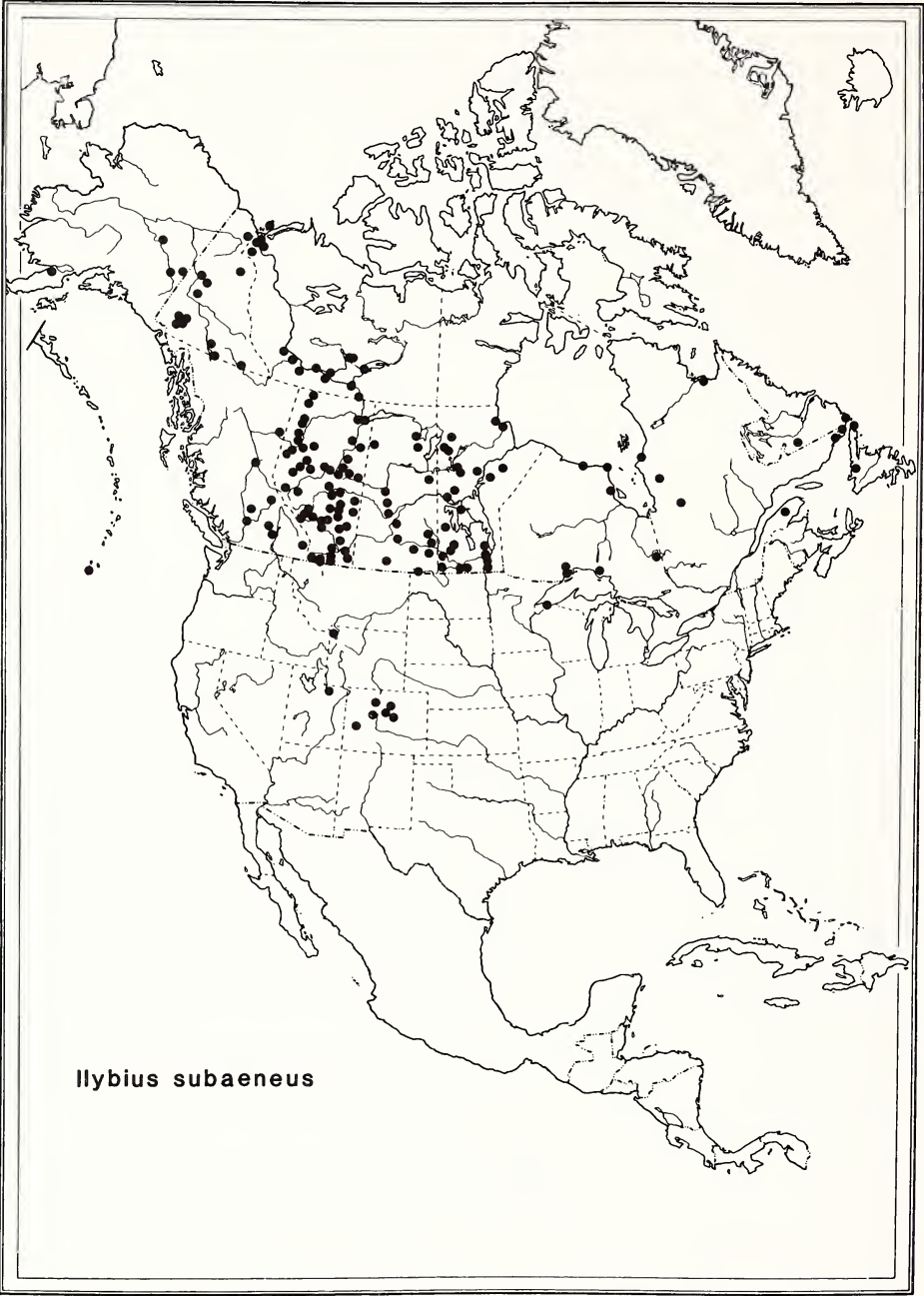
in form of short fine striae. Metatibia with coarse punctures along length of ventral face. Longer metatibial spur subequal in length to metatarsomere 1. Metatarsomeres lacking coarse dorsal and ventral setae.

MALE: Protarsal claws as in Figure 44, posterior claw narrow, ventral emargination broad and subbasal. Metacoxae with a short longitudinal keel on posterior portion of medial line. Metatarsomeres 1 to 3 with a dorsolateral bead: metatarsal claws as in Figure 58, dorsal claw broadly arcuate and tapering to apex. Sternum 6 (Fig. 25) with numerous coarse longitudinal rugae along posterior margin, these rugae obscuring setiferous punctures: a distinct medial longitudinal keel lacking; lateral bead obsolete across rugose portion of sternum. Subgenital plate broadly rounded to subtruncate apically, it and lateral plates coarsely longitudinally rugose. Genitalia (Fig. 72) with paramere bearing numerous adhesive setae along mesal face: aedeagus short, apex simple.

FEMALE: Metatibia with mesal margin and metatarsomeres with lateral margin lacking natatorial setae. Sternum 6 (Fig. 31) emarginate medially, lateral bead continuous around lateral angles of emargination.

Variation. Most specimens have a distinct metallic, usually green (sometimes coppery), sheen. Specimens with reduced, or lacking, metallic reflection occur so that color alone is not a reliable diagnostic character. Specimens in a series from Lake Nipigon, Ontario (Macdiarmid, ROM), have the lateral margins of the body broadly pale, with the pale area extending mesad of the sublateral vittae on some specimens and obscuring it. Very pale specimens of *I. confusus* (described by Wallis as *I. denikei*) also occur in the same general region, thus there appears to be an environmental factor promoting development of pale forms of *Ilybius*. The type specimen of *I. suffusus* Crotch has the lateral margins of the body broadly pale as described above.

Mean size varies among population samples (Table 13). The smallest specimens



Map 11. North American collection records for *Ilybius subaeneus*.

seen were from the northwest (northern B.C.; Reindeer Depot, N.W.T.), while specimens with the largest mean size were from Colorado. A clear geographical pattern in size variation is not evident and perhaps most variation is ecotypic. Samples from boreal sites have similar mean sizes while specimens from the prairies and eastern alpine sites average a little smaller.

Mean values for the ratios, L/W and WC/WS vary slightly among populations but in different patterns than that shown by length. Four Finnish specimens that I measured fell within the range of values observed among North American specimens.

Nomenclatural notes. *Ilybius viridianus* Crotch is listed as a synonym although the type was not examined. I did not locate it while examining the LeConte collection. Crotch's description includes the salient characters for species recognition so there is little doubt about this synonymy.

Classification notes. This species is most similar to *I. pleuriticus* and in fact some female specimens cannot be assigned to one species or the other with certainty.

Ecology. This species occurs in shallow, sun-warmed, usually permanent or semi-permanent lentic habitats. Specimens occur among emergent vegetation in both forest and grassland ponds. In Labrador, specimens are found principally in shallow water along sheltered lake shores, either among emergent plants or frequently on bare gravel or sand substrates. The larva has been described (Balfour-Browne, 1950; Nilsson, 1982). I have seen a single record of flight, 26 July.

Distribution. The species is holarctic. The North American range extends from the Northern Peninsula of Newfoundland, to the Aleutian Islands, Alaska, and in the west from the Mackenzie Delta to alpine areas of Colorado (Map 11).

SPECIES ERRONEOUSLY RECORDED FROM NORTH AMERICA

Several palaearctic species have been recorded from North America, or are represented in collections by specimens purported to be of North American origin. I consider the following species to be incorrectly attributed to North America because the records are based on single, old specimens with incomplete collection data and the occurrence has not been substantiated by recent, reliable records.

Ilybius ater (DeGeer, 1774)

Colymbetes unguicularis LeConte 1862:521 (Type examined—specimen in MCZ labelled: pink disc/"C. unguicularis Lec."/"/"Type 6039"/"/"I. unguicularis LeC. ater = Crotch") is a junior synonym of *I. ater* as stated by Crotch (1873). There is a second male in MCZ labelled "Indiana, Pa." I believe Wallis (1939) was correct in rejecting this as an American species.

Ilybius fenestratus (Fabricius, 1781)

This species was recorded from North America in some of the older literature, probably due to misidentification or misinterpretation of names (Balfour-Browne, 1950). There is a specimen in USNM labelled "Br. Col.," but the species is certainly not North American.

Table 14. Characters used in phylogenetic analysis of species of *Ilybius*. P—Plesiotypic state; A(n)—apotypic states(s).

Character	State	Description	Basis of comparison
1. Male genitalia sternum 9	P	oval plate with apex broad, rounded, truncate or bilobed	generalized ex-group
	A1	oval plate narrowly pointed apically	
	A2	oval plate with apex broadly rounded with a deep semicircular median notch	
2. Male genitalia aedeagus	P	basal guards well developed and semicircular	generalized ex-group
	A	guards small	
3-1. Male sternum 6	P	smooth, without longitudinal rugae	generalized ex-group
	A1	hind margin longitudinally rugose	
	A2	secondarily smooth through loss of rugae (some specimens with rudiments of rugae)	in-group
3-2. Male sternum 6	P	without posteriomedial longitudinal carina	generalized ex-group
	A1	medial carina present	
	A2	carina lost	in-group
4. Female	P	distinct V-shaped posteriomedial notch	generalized ex-group to determine plesiotypic state and in-group to establish direction of transformation
5. Metatibia, punctuation of ventral surface	A	notch shallow	
	P	coarse punctures present along length	generalized ex-group
	A	middle and distal portions impunctate or micropunctate	
6. Color of dorsal surface	P	dark dorsally, grading to paler lateral margins	generalized ex-group
	A1	broad, sharply defined lateral margins	

Table 14. Continued.

Character	State	Description	Basis of comparison
7. Habitus	A2	lateral margins broadly pale but gradually darkening onto disc	in-group, generalized body form throughout genus. Apotypic states based on in-group comparisons
	P	body oval, narrowed anteriorly and more so posteriorly, dorsally strongly convex	
	A1	body more elongate and dorsally flattened	
	A2	body broader, depressed	
	A3	body broader and more rounded in dorsal aspect	
8. Posternal process	P	elongate, metasternal emargination extending to level of hind margin of mesocoxal cavities	generalized ex-group
	A	short, metasternal impression not attaining level of hind margin of mesocoxal cavities	
9. Elytral sculpture, punctation	P	punctures present at intersections of lines of primary sculpture	generalized ex-group
	A	punctures absent from intersections	
10. Male genitalia, paramere	P	parameres slender without subapical shoulder	generalized ex-group
	A	paramere broader, subapical shoulder prominent	
11. Male genitalia parameres	P	suckers absent from mesal face	generalized ex-group
	A1	suckers present	
	A2	suckers absent (secondarily) with patches of dense coarse setae in similar positions	

Table 14. Continued.

Character	State	Description	Basis of comparison
12. Female, metatibia and metatarsi	P	natatorial setae lacking from inner face of metatibia and outer surface of metatarsomeres	generalized ex-group
13. Male genitalia, aedeagus	A	natatorial setae present	generalized ex-group. Species specific forms considered apotypic
	P	subequal in length to parameres, symmetrical apex evenly narrowed	
	A1	elongate, apex flattened and recurved	
	A2	apex hooked	
	A3	apex with short lateral flanges, spear-shaped	
14. Male, metatarsus	A4	apex narrow, slightly reflexed	generalized ex-group
	P	dorsolateral bead absent	
15. Metacoxal wing	A	dorsolateral bead present	generalized ex-group
	P	broad, $WC/WS < 3.5$	
16. Elytral sculpture, primary meshes	A	narrow, $WC/WS > 3.5$	generalized ex-group; in-group for apotypy of species states
	P	meshes of more or less similar form over disc of various species or lines deeply impressed	
	A1	meshes granular	
	A2	meshes strongly elongated basally and medially on disc	
	A3	meshes irregularly fused and elongated	
17. Size	P	average size for genus	in-group
	A1	reduced size in lineages with sister taxa near average size	
	A2	increased size in lineages with sister taxa near average size	

Table 14. Continued.

Character	State	Description	Basis of comparison
18. Metacoxal plate sculpture	P	strioles well developed and intersecting	ex-group
	A	strioles reduced, short and separate or absent	in-group
19. Antenna, palpi color	P	entirely pale	in-group (infuscation widespread in agabines but of limited distribution in <i>Ilybius</i>)
	A	apical infuscation present	
20. Elytron, color	P	piceous or black, without metallic sheen	ex-group
	A	with metallic brass or green sheen	
21. Female, sternum 6	P	marginal bead complete around lateral angle of medial emargination	in-group
	A	marginal bead obsolete on lateral angle of medial emargination	
22. Metafemur, punctures	P	punctures rounded	ex-group and in-group
	A	some punctures along hind margin elongate, striolate	

Ilybius fuliginosus (Fabricius, 1792)

Balfour-Browne (1950) reviewed the history of North American records and concluded they were probably due to misidentification of various North American species. There is a male specimen of *I. fuliginosus* labelled "Pa." in MCZ and a male specimen labelled "Ind." in CNC but lack of supporting records suggests these are cases of mislabelling.

PHYLOGENETIC CONSIDERATIONS

The taxonomic placement of the genus *Ilybius* has been discussed in a general way in the introduction. Although a more comprehensive study is required to determine its systematic position and to identify its sister taxon, present evidence strongly supports placing *Ilybius* in the tribe Agabini. Monophyly of the genus is clearly established by the synapotypic female ovipositor of the included species.

For purposes of deducing phyletic relations, generalized ex-group comparison of characters have been used to develop hypotheses regarding plesiotypic states. These comparisons were made between the species of *Ilybius* and other agabines, especially those members of *Agabus* that possess the plesiotypic character of an incompletely margined clypeus (Larson, 1975). In-group (between the species of *Ilybius*) comparisons were used for estimating direction of character change for those characters which have limited distribution among taxa of *Ilybius*. If two sister taxa differ in the states of a character, the state occurring in their sister clade is considered plesiotypic. Some character states are considered to be apotypic if the taxa bearing them are apotypic in a number of other features.

Descriptions of the characters used in this analysis, the character states recognized, and the rationale used in deducing direction of character transformation, are presented in Table 14. Interpretation of certain of these characters is problematical: such characters are discussed in more detail in the following section.

DISCUSSION OF CHARACTER STATES

The characters used in the phylogenetic analysis are those of diagnostic value in the definition of taxa and have been described in the generic and species descriptions. Many of these characters occur in two states with the derived state apparently evolved once. Some characters show several states or the distributions of character states suggest convergence or reversals. Such characters are discussed below where rationale for interpretation of the character states is given. Reference is made in the character state discussions to points in the cladogram (Fig. 75) where specific states appear. Capital letters refer to the similarly labelled bifurcation points in the cladogram while lowercase a and b refer to left and right branches respectively.

Characters 3.1 and 3.2—male sternum 6. The sculpture of the hind margin of the sternum is highly varied among species of the genus and affords some of the best characters for species recognition. The sculpture consists of the presence or absence of longitudinal rugae, a medial longitudinal keel (carina) or both in various combinations. I interpret the medial carina as secondarily derived from the rugose sculpture through the narrowing and raising of a medial ruga. I make this interpretation because I know of no other agabine outside of *Ilybius* that possesses an abdominal keel although several species of *Agabus* possess longitudinal rugae. A keel is present in a number of groups of *Ilybius* where rugae are also widespread among the group

6 of members of the *I. apicalis* group is plesiotypic. The lack of rugae in members of the *I. biguttulus* group is regarded as a secondary loss because some members of the group possess a median keel, which being derived from rugae would mean that an ancestor possessed rugae. As all species of *Ilybius* other than those of the *I. apicalis* group have either rugae, a medial keel or show strong affinity with species that do, I conclude the stock common to all *Ilybius* exclusive of the *I. apicalis* group possessed at least a rugose sternum 6 (Ab, 3-1A1). Subsequent modification of this state was loss of medial rugae (Ba, 3-1A2), the development of a medial keel with rugae present (Cb, 3-2A1), or loss of various elements of this system, e.g., rugae present, carina secondarily lost (Jb, 3-2A2), carina present and rugae lost (Ja, 3-1A3), or rugae and carina secondarily lost (Ib, 3-1A2, 3-2A2).

The median keel appears in lineages after the initial acquisition of rugae (Cb, 3-2A1). The occurrence of the keel in *I. biguttulus* and *I. ignarus* is difficult to explain. The model presented here involves two independent acquisitions of a medial keel (Cb, Ia, 3-2A1). The alternative, the common origin for the keel from Bb, would require postulation of secondary losses at Da, Fa and Ib. Parsimony was the basis for choosing the pattern presented but parallel independent losses is more probable than parallel independent acquisitions of a character, given similar numbers of transformations.

Character 4—female sternum 6. The medioapical emargination is a synapotypy that unites the members of the genus and is correlated with the possession of saw-like gonocoxae. The emargination is deep and V-shaped in most species but in members of the *I. apicalis* group (Aa) the notch is very small. Although not so reduced as in the *I. apicalis* group, the emargination is relatively shallow in the *I. biguttulus* group (Db) as well as in several palaearctic members of the *I. angustior* (Eb) group. The character is gradational and difficult to assess.

Character 5—Metatibia, punctation of ventral face. All *Ilybius* species have punctures on the ventral face of the metatibia, but the size and distribution of punctures varies considerably among (sometimes even within) species. It is postulated that the plesiotypic state is coarse punctures along the length of the ventral face. From this state, parallel losses of coarse punctation occur at Aa, Ca and Ga. *Ilybius pleuriticus* specimens show reduced size and numbers of punctures and suggest an intermediate stage towards loss (Ja).

Character 6—color of dorsal surface of body. Specimens of *Ilybius* are basically dark (piceous or black) beetles in which the margins of the body are variously paler. Members of the *I. apicalis* group have broad yellow margins to the pronotum and elytra with these margins abruptly limited to the disc (Aa, 6A1): the venter is reddish yellow. This color pattern also occurs in *I. fuliginosus* which belongs with species of clade Eb. Broad but gradually paler lateral margins (6A2) occur in *I. pleuriticus*, *I. confusus* and some populations of *I. subaeneus*.

Character 7—habitus. Most *Ilybius* are recognizable on habitus as their bodies are narrowly rounded both towards the head and even more so apically, while in lateral aspect they are strongly convex dorsally and flattened ventrally. Modifications of this form are shown by: members of the *I. apicalis* group which are elongate and flattened (Aa, 7A1) and *I. vittiger* which is broad and depressed (Hb, 7A2). Members of the *I. biguttulus* group (Db) tend to be broader in outline than members of the *I. angustior* group (Cb) but the differences are slight and exceptions occur among species in each group so that the character is equivocal for phylogenetic analysis.

Character 8—prosternal process. Length of the prosternal process varies among species of the genus. An elongate prosternal process that is received into a deep emargination of the metasternum (extending posteriorly to at least level of hind margin of mesocoxal cavities) is considered plesiotypic. Shortening of the process occurs independently in *I. lateralis* (palaeartic), *I. vittiger* and *I. oblitus* and to a lesser degree in *I. churchillensis* and as such is associated with elongation, flattening or broadening of the body. The functional significance of shortening of the process is not apparent although it would appear to permit increased flexibility of the prothorax enhancing crawling or burrowing capability but probably with reduced swimming efficiency.

Character 13—male genitalia, aedeagus. The form of the aedeagus tip varies among species and provides some good diagnostic characters for species recognition. However, the generally similar form throughout the genus provides few good characters for defining supraspecific groupings.

Character 15—metasternal wing. The width of the lateral portion of the metasternum varies considerably. Through generalized ex-group comparison, the plesiotypic condition is believed to be broad (WC/WS—2.00 to 3.50). Narrowing occurs in several separate lineages, most strongly so in Fa and to a lesser degree, Na as well as in several palaeartic species. The character is most useful for species diagnosis. The significance of the narrowed metasternal wing is not known but it has been postulated as being related to reduced flight capability (Jackson, 1952).

Character 16—elytral sculpture. Two levels of sculpture occur on the elytra which in the terminology of Larson (1975) are: primary—coarsest lines and the meshes or interspaces between them; and secondary—which is comprised of much smaller and finer lines which produce a fine, reticulate sculpture on the meshes of the primary sculpture. The secondary sculpture is more or less consistent throughout the genus and varies mainly in the degree of effacement of lines which occurs on most specimens on the basal or medial portions of the elytral disc. Variation in the primary sculpture occurs as: deepening of lines so that meshes appear more raised or granular (16A1); longitudinal stretching or elongation of meshes (16A2); or fusion of adjacent meshes due to short sections of the primary lines disappearing (16A3). State 16A2 is best developed in lineages Da and Ib but it also suggested in some specimens of *I. biguttulus* (Ma).

Character 17—size. Although all members of the genus are moderately large dytiscids, size varies considerably between species. Size variation probably has more of an ecological than phylogenetic basis. For example, the smallest species, *I. discedens*, *I. vittiger* and *I. ignarus* are peat pool species, while the largest species are those most frequently found along the margin of larger water bodies, e.g., *I. pleuriticus* and *I. confusus*.

PHYLOGENY OF NORTH AMERICAN SPECIES OF *ILYBIUS*

The cladogram presented in Figure 75 diagrammatically represents phyletic relationships hypothesized among North American and select palaeartic species of *Ilybius*. The palaeartic species, *I. apicalis* and *I. cinctus*, are included as they appear to be the sister group (Aa) to all other *Ilybius*. The name *Agabidius* Seidlitz is available for this clade which I consider distinct enough to warrant subgeneric rank.

The two species of clade Ba, *I. discedens* and *I. vittiger*, are small, northern, peat pool species. They possess a number of characteristics in common but as discussed above, most of these are synplesiotypies so the relationship may not be very close. Differences in such features as habitus, aedeagus, female sternum 6, and natatorial setae on the hind legs of female *I. discedens*, suggest relationship is distant. While *I. discedens* is phyletically isolated and possesses enough distinctive features to be placed in a subgenus separate from the members of clade Bb, *I. vittiger* is in some ways bridging. I feel introducing subgeneric ranking for a species of such uncertain phyletic relationships to be inadvisable at present.

Clade Cb is a well defined, apparently monophyletic group characterized by males with the synapomorphic laterally beaded metatarsomeres. This group contains six North American species, half of which are holarctic, as well as the majority of the palaearctic species.

Clade Ca is less certainly monophyletic for the group is based largely on negative or plesiotypic characters. The species of clade Db are a natural group as evidenced by the very similar male genitalia. The members of this clade are North American with no close palaearctic relatives. The North American range is centered mainly in the northern Appalachian region but one species, *I. biguttulus*, extends into the southeastern boreal region as well as across the central plains into the southern Rocky Mountains. The position of *I. fraterculus* is enigmatic. The lack of suckers on the parameres, the apically hooked aedeagus and the deeply emarginate female sternum 6 separate this species from the other members of clade Ca. On the other hand, these male characters as well as the tendency for the primary elytral sculpture to be longitudinally stretched also separate the species from the members of clade Cb. For the present, the position of *I. fraterculus* as the western North American sister species to the stem of clade Db seems to be the best solution to its placement.

Two peculiar palaearctic species, *I. fenestratus* and *I. similis*, belong in clade Bb but differ from the members of both clades Ca and Cb on a number of features and are not obvious sister taxa of either. Their placement is discussed in the following section.

The remaining relationships are discussed under the individual species accounts and indicated in Figure 75 and need no additional explanation.

SYSTEMATIC NOTES ON PALAEARCTIC SPECIES

Ilybius aenescens Thomson, 1870:125.

Plesiotypic Characters—1, 2, 4, 6, 7, 8, 12, 13, 15, 17, 19, 20, 21.

Apotypic Characters—3-1A2, 3-2A1, 9, 10, 11A1, 14, 18.

Variable Characters—5, 16, 22.

Topological Position—This species shares many similarities with the taxa of branch Eb but lacks infuscation of antennae and palpi, shows reduction or loss of male sternum 6 rugae, reduced metacoxal plate striae, reduced metatibial punctation and a longitudinal stretching of basomedial elytral meshes. This is probably the sister taxon of clade Gb.

Ilybius apicalis Sharp 1873:51.

The phylogenetic interpretation of character states of this species are indicated in Figure 75. Zaitzev (1953) and Leech (1955) consider *I. apicalis*, *I. cinctus* Sharp and

I. lateralis (Gebler) to be closely related. I recognize the close relationship between *I. apicalis* and *I. cinctus* but regard the similarities with *I. lateralis* as convergent (see *I. lateralis* below).

Ilybius ater (DeGeer 1774:401).

Plesiotypic Characters—1, 2, 4, 5, 7, 8, 12, 15, 18, 19, 20, 21.

Apotypic Characters—3-1A2, 3-2A1, 6A2, 9, 10, 11A1, 17A2, 22.

Variable Characters—16.

Topological Position—This is the largest species of the genus. The aedeagus is diagnostic, long and slender with basal piece bent at an angle greater than 90° from longitudinal axis of shaft. Strioles of the metatibia are very strongly developed. Elytral sculpture is sexually dimorphic with the male form plesiotypic. This species possesses the apotypic characters of clade Ea and appears to be the palaearctic sister species of *I. pleuriticus* (Ja).

Ilybius cinctus Sharp 1882:560.

The phyletic position of this species is indicated in Figure 75 and discussed under *I. apicalis* above. Zaitzev (1953) regards *I. angustulus* Regimbart 1899:289, and *I. chinensis* Csiki 1901:102, to be junior synonyms of *I. cinctus*.

Ilybius crassus Thomson 1856:224.

Plesiotypic Characters—1, 2, 4, 5, 6, 8, 12, 13, 15, 17, 18, 19, 20.

Apotypic Characters—3-1A1, 3-2A1-A2, 7A3, 9, 10, 11A1, 14, 16A1-A2, 21, 22.

Topological Position—Male sternum 6 longitudinally rugose but rugae more or less obsolete medially (convergent with clade Ba), lacking a distinct keel but with a medial tumid area interpreted as an obsolete keel. The aedeagus is short and blunt and similar to that of *I. pleuriticus*. Lines of elytral sculpture are deep and meshes slightly elongate, especially on female. The species is closest to clade Ea. *Ilybius weymarni* Balfour-Browne 1947 is very similar and the name is probably a junior synonym of *I. crassus*.

Ilybius fenestratus (Fabricius 1781:294).

Plesiotypic Characters—2, 4, 12, 14, 17, 19, 21.

Apotypic Characters—1A2, 3-1A1, 3-2A1, 5, 6A2, 7A3, 8, 9, 10, 11A1, 13, 15, 16A3, 18, 20, 22.

Topological Position—This species and *I. similis* (see below) occupy a rather isolated position within the palaearctic fauna. They are best placed in the cladogram at node C but they possess such a unique combination of plesiotypic and apotypic characters that they do not fit into either clade Ca or Cb. They probably represent a sister group to clade Cb. In addition to the characters enumerated above, other species specific features are: elytron with meshes of primary sculpture irregular but with some tendency for transverse stretching; and aedeagus very elongate.

Ilybius fuliginosus (Fabricius 1792:191).

Plesiotypic Characters—1, 2, 4, 8, 12, 13, 15, 16, 17, 19, 22.

Apotypic Characters—3-1A1, 3-2A1, 5, 6A1, 7A1, 9, 10, 11A1, 14, 18, 20, 21.

Topological Position—Color is similar to that of taxa of clade Aa, but most structural characters including the laterally beaded male metatarsomeres and male genital

characters place the species in the clade Cb. *Ilybius meridionalis* Aube 1836:126, a species found in the Mediterranean region, is similar in all characteristics except it possesses narrower metasternal wings.

Ilybius guttiger (Gyllenhal 1808:499).

Plesiotypic Characters—1, 2, 4, 6, 7, 8, 12, 13, 15, 16, 17, 18, 19, 20, 21, 22.

Apotypic Characters—3-1A2, 3-2A1, 9, 10, 11A1, 14.

Variable Characters—5, 16.

Topological Position—This species very closely resembles *I. aenescens* occupying a similar position in the cladogram.

Ilybius lateralis (Gebler 1832:40)

Plesiotypic Characters—1, 2, 9, 10, 12, 13, 15, 16, 19, 20, 21, 22.

Apotypic Characters—3-1A2, 3-2A2, 4, 5, 6A1, 7A1, 8, 11A1, 14, 17A1, 18.

Topological Position—This species is difficult to place as it possesses a very peculiar combination of characters. In general habitus, as well as in many specific details, it resembles specimens of clade Aa, with which it was associated by Zaitzev (1953) and Leech (1955). Male characters such as laterally beaded metatarsomeres, and parameres with suckers, place it in clade Cb. The shared similarities with members of clade Aa are probably convergent.

Ilybius obtusatus Sharp 1882:558.

Plesiotypic Characters—4, 5, 6, 7, 9, 12, 15, 16, 17, 18, 20, 21, 22.

Apotypic Characters—8, 19.

Topological Position—I have seen only the female holotype, thus male characters have not been scored. Based on female characters, the species is most similar to members of clade Ba. This implies the males should have the following characters: metatarsomeres lacking lateral bead; parameres without a defined shoulder and lacking suckers; and sternum 6 with rugae posteriolaterally, smooth medially and lacking longitudinal carina. Zaitzev (1953) described the male as having laterally ridged metatarsomeres and sternum 6 with a weak medial keel and strong lateral rugae. It is possible that Zaitzev's description applies to another species, but it he was correct the peculiar combination of characters will necessitate a reevaluation of the position of clade Ba.

Ilybius quadriguttatus (Lacordaire 1835:316).

Plesiotypic Characters—1, 2, 5, 6, 7, 8, 12, 13, 15, 16, 18, 19.

Apotypic Characters—3-1A2, 3-2A1, 4, 9, 10, 11A1, 14, 17A2, 21, 22.

Topological Position—The male genitalia and margined metatarsomeres place this species in clade Cb. The larger than average size, pale antennae and palpi and striolate punctures of the metafemur indicate an affinity with clade Ea. The emargination of female sternum 6 is shallow for members of this group. A species-specific character of the male is the presence of an usually distinct tooth medially situated on the ventral margin of the posterior protarsal claw.

Ilybius similis Thomson 1856:225.

Plesiotypic Characters—2, 4, 5, 6, 7, 8, 12, 13, 14, 15, 17, 18, 19, 20.

Apotypic Characters—1A2?, 3-1A1, 3-2A1, 9, 10, 11A1, 21.

Variable Characters—16, 22.

Topological Position—This species shares many features (both plesiotypic and apotypic) with *I. fenestratus* and is probably its sister species. Together these species are rather isolated from other species of *Ilybius*. Male sternum 9 is very broad, as in *I. fenestratus*, but has only a small apical emargination as opposed to the deep semicircular notch of *I. fenestratus*. In spite of this difference, both are considered to represent the same character state.

ACKNOWLEDGMENTS

I thank the following individuals for loaning me specimens of *Ilybius* or for showing me hospitality during my visits to their collections: Dr. D. Azuma (ANSP), Mr. M. E. Bacchus (BMNH), Mr. S. Cannings (UBC), Mr. and Mrs. J. L. Carr (CARR), Mr. C. Chantal (CHANT), Dr. P. Harper (UMC), Dr. D. Kavanaugh (CAS), Dr. J. Matta (ODU), Dr. A. F. Newton, Jr. (MCZ), Dr. C. L. Remington (PMYU), Dr. G. Scherer (ZSM), Dr. A. Smetana (BRC), Dr. P. J. Spangler (USNM), Dr. G. Wiggins (ROM), Dr. W. Wolfe (CCRU), and Dr. J. R. Zimmerman (NMSU).

Drs. Wm. Hilsenhoff (University of Wisconsin, Madison), A. N. Nilsson (University of Umea, Umea) and G. W. Wolfe (CCRU) reviewed a draft of this paper and provided many valuable criticisms and comments. The paper has been greatly improved by this assistance. Also, Wm. Hilsenhoff most generously provided Wisconsin collection records as well as data on ecology.

I thank Mr. E. Rickey (BRC) for his assistance in preparing the scanning electron micrographs, Ms. Juby Au for inking the line drawings, and Ms. L. Collins for preparing the distribution maps.

I am especially grateful to the Natural Sciences and Engineering Research Council of Canada for making this study possible through an individual operating grant (grant no. A6192) and a travel grant.

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Received September 15, 1986; accepted May 7, 1987.